Conservation in human-influenced areas:
epigaeic arthropods in the Cape Floristic Region lowlands

by

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Thesis presented in partial fulfillment of the requirements for the degree of Master of Science (Conservation Ecology), in the Faculty of AgriSciences, University of Stellenbosch

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December 2006

DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis 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 conservation of biodiversity is becoming increasingly challenging as habitats are disturbed, fragmented or destroyed. Although nature reserves now cover more than 10 % of the earths' surface it has become clear that more will have to be done to ensure the long-term survival of species. Therefore, focus is increasingly shifting towards conserving biodiversity in natural and semi-natural remnants in human-influenced areas. This study aimed to determine the contribution of remnants in human-influenced areas to the conservation of biodiversity in the Cape Floristic Region (CFR) lowlands, using ground-dwelling arthropods, specifically ants, as the focal taxon. Initially, base-line information of arthropods and in particular ants was obtained. Sampling arthropods generally involves a large sample effort. Therefore maximizing sampling effort for ants in the CFR was investigated by trapping ground-dwelling ants at a single locality. Doubling the number of grids of pitfall traps was found to be more effective in trapping a greater number of species than doubling the duration of sampling. Therefore increasing spatial sampling intensity rather than sampling duration maximizes sample effort for CFR ants. Also, the seasonal changes of ground-dwelling arthropods, including ants, were determined by sampling four times during the year at a single locality. Overall arthropod abundance was found to peak in summer while dropping to a minimum in winter. This pattern was mirrored by that of the ants, indicating that ant results have a broader relevance than to ants only. The ground-dwelling fauna was dominated by ants emphasizing their importance in the CFR lowlands, and demonstrating that ants are an appropriate flagship taxon for epigaeic arthropod diversity in the CFR. Finally the contribution of remnants in human-influenced areas to the conservation of the CFR was investigated. A nested hierarchical approach was used, where five localities were selected across the CFR, each containing one reserve site and one site with natural remnants. Ants were sampled, along with environmental variables, namely weather, vegetation and soil. Overall, remnants were found to support similar ant assemblages to those of reserves. However for individual localities some remnants were significantly different to their reserve counterparts. Differences in ant assemblages were found to be greater between localities than between reserves and remnants. The relatively high heterogeneity of ants

found in this study emphasizes the conservation significance of invertebrates along with that of plants in the CFR. Remnants clearly show the potential to conserve ant assemblages, however correct management is needed for these areas to maximize their potential. Disturbances such as the presence of the invasive Argentine ant and increasing soil nutrients by fertilization, pose a distinct threat to the ability of remnants to conserve ant assemblages. This study has shown that remnants currently support ant assemblages representative of those present in the CFR today. Therefore, some remnant patches of habitat in agricultural areas currently do contribute highly to the conservation of a functional important taxon in this global biodiversity hotspot, and if managed correctly, may continue to do so in the future.

OPSOMMING

Die vernietiging en fragmentering van habitatte maak die bewaring van biodiversiteit al hoe meer van 'n uitdaging. Alhoewel natuur reservate reeds meer as 10 % van die aarde se oppervlak beslaan is dit duidelik dat meer gedoen sal moet word vir die lang-termyn voortbestaan van spesies. Dus word die fokus van biodiversiteit-bewaring toenemend gerig op bewaring van natuurlike en semi-natuurlike fragmente in menslik-beinvloede gebiede. Die doel van hierdie studie was om te bepaal wat die bydrae van fragmente van natuurlike veld in menslik-beinvloede gebiede is tot die bewaring van die streek. Dit is gedoen deur van grond-lewende geleedpotiges en spesifiek, miere in die Kaapse floraryk (CFR) gebruik te maak. Aanvanklik is kennis ingewin oor die geleedpotiges en spesifiek miere in die omgewing. Omdat die versameling van geleedpotige diere gewoonlik baie moeite vereis is 'n maksimum steekproef gedoen by 'n enkele lokaliteit. Daar is gevind dat 'n verdubbling van die aantal ruitsteekproefnemings met vanggate meer effektief is om miere te vang as 'n verdubbling in die tydperiode wat vanggate oop is. Dus, is 'n hoër ruimtelike steekproef intensiteit meer effektief in vergelyking met 'n langer tydsduur vir miere in die CFR. Die seisoenale veranderinge van grond-lewende geleedpotiges, sowel as miere, was ook bepaal. Dit was gedoen deur vier seisoenale steekproewe te doen by 'n enkele lokaliteit. Die totale geleedpotige-talrykheid was die meeste gedurende die somer en die minste in die winter. Die miertalrykheid het ook hierdie patroon weerspieël. Dit dui daarop dat veranderinge in mier versamelings van breër belang is vir alle grond-lewende geleedpotiges. Miere was die dominante grond-lewende geleedpotiges en beklemtoon die belangrikheid van miere in die CFR, sowel as hulle toepaslikheid as vlagskip taksa vir grond-lewende geleedpotige diversiteit in die CFR. Laastens was die bydrae van gefragmenteerde natuurlike veld in menslik–beinvloede gebiede tot die bewaring van die CFR ondersoek. 'n Krimpende/ genestelde hiërargies benadering is gebruik in vyf geselekteerde lokaliteite, elk het bestaan uit 'n area in 'n natuur reservaat en 'n area in 'n naasliggende fragment. Miere was versamel saam met 'n verskeidenheid omgewings veranderlike, naamlik weer, plantegroei en grond. In die algemeen is gevind dat fragmente en reservate gelyksoortige mier versamelings het. Daar was wel gevind dat party fragmente aansienlik verskillend was van die reservaat teenstuk. Verskille in mier

versamelings tussen lokaliteite was groter as verskille tussen reservate en fragmente. Die relatief hoë heterogeniteit van miere beklemtoon die bewaringsbelang van invertebrate saam met dié van plante in die CFR. Dit is duidelik dat fragmente wel 'n potensiale bydrae kan maak om die mier versamelinge te bewaar, maar gepaste bestuur is nodig om hierdie potentiaal te maksimaliseer. Versteurings soos die teenwoordigheid van die indringer Argentynse mier en toenemende grondvoedingstofkonsentrasie as gevolg van bemesting is 'n groot bedreiging tot die vermoë van fragmente om mier versamelings te bewaar. Hierdie studie wys dat mier versamelings in gefragmenterde areas verteenwordigend is van die algemene mier versamlings wat op die oomblik in die CFR is. Dus lewer party fragmente in landbou gebiede op die oomblik 'n wesenlike bydrae tot die bewaring van 'n funksioneel belangrike takson in hierdie globale biodiversiteitsbrandpunt en die bydra sal volhoubaar wees met korekte bestuur.

ACKNOWLEDEGEMENTS

Firstly, I thank my supervisor, Melodie McGeoch, for trying her very best to mould me into a real researcher. For all her efforts, patience and encouragement I am very grateful. I have attained much higher standards than I believed I was capable of. Thanks also to Kate Parr, for help with the ant identification and valuable input and comments on many draft versions.

To all the managers and staff of the following Nature Reserves, Elandsberg, Riverlands, Pella, Hottentots-Holland, Jonkershoek and Helderberg as well as farm owners and managers of the farms in the various regions, Elandskloofberge, Grabouw, Stellenbosch and Somerset West, for permission to sample on their property and assistance given, thank you very much. I also thank the AgroMet-ISCW Agricultural Research Council for their excellent service and providing weather data.

I thank the National Research Foundation (under Grant number GUN2053618), BIOTA program (funding provided by the BMBF (01LC 0024A)) as well as the University of Stellenbosch and the Harry Crossley Foundation for financial assistance.

A big thank you goes to the many people who assisted me. I'm grateful to Sonja and especially Peter for many hours of help in the field, Antoinette for additional assistance with ant identification and Lorenzo Prendini for solifugae and scorpion identification. For assistance with computer programs I thank Cang (beta-diversity calculations) and Thomas Crist (PARTITION software). To my fellow ConsEnt spacers and Sonja, thank you for the many laughs and continual advice and help.

To my husband, Leandro, who lived through many a moan session, thank you for your patience, prayer, understanding and encouragement, for reading through my ecology gibberish and loving me to bits. I thank my parents for instilling a passion for nature in me and for their unending support and love and the many sacrifices to give me a good education. My sisters and friends I thank for keeping me balanced and for providing loads of delightful distractions.

Most importantly I thank my Father in heaven for His unfailing love for me. I know that the only reason I made it through this Masters is because He believes in me and His grace IS always sufficient for everything!

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The conservation of biodiversity is becoming progressively more challenging as the human population continues to expand, and with it the demand for resources (Chown *et al.* 2003, Rouget *et al.* 2003). Agriculture, pollution and resource withdrawal have and continue to transform vast amounts of land (Bestelmeyer & Wiens 1996, Laurance & Cochrane 2001) leaving behind disturbed habitat patches scattered across the landscape in various shapes and sizes (Saunders *et al.* 1991, Banks 2000). Indeed the correlated processes of habitat loss and fragmentation are described as the most important ongoing threats to biodiversity (Laurance & Cochrane 2001, Tscharntke *et al.* 2002). At the same time, the number of protected areas has increased exponentially since the 1900s and reserves now cover around 13.2 million km^2 of the earth's surface (Gaston & Spicer 2004). However it has become clear that protected areas alone will not prevent global biodiversity loss (Rodrigues *et al.* 2004) and hence conservation is increasingly shifting to focus on and include areas outside of protected areas (Knight 1999, Norton 2000, Goodman 2003, Solomon *et al.* 2003, Dudley *et al.* 2005).

Problems with current protected areas and reserve networks include the suboptimal layout of reserves, i.e. they are poorly sited with little planning to optimize their conservation value, especially in the face of climate change, and they are mostly too small to sustain the long-term survival of viable populations (Saunders *et al.* 1991, Margules & Pressey 2000, Reyers *et al.* 2002, Chown *et al.* 2003, Goodman 2003, Gaston & Spicer 2004, Opdam & Wascher 2004). Additionally, reserves are often incompatibile with surrounding land-uses resulting in alien vegetation encroachment and poaching by neighboring human community members (Pimentel & Stachow 1992, Reyers *et al.* 2002, Goodman 2003). Prospects of gaining sufficiently more land for formal reserve networks to be effective is improbable due to the increasing and conflicting demand for land by a growing human population and lack of sufficient available funds (Perrings *et al.* 2006). The possibility of establishing links to other areas of protected or conserved land in order to increase the conservation status of protected areas is frequently unattainable, or where this is feasible these areas are privately or

communally owned (Chown *et al.* 2003, Perrings *et al.* 2006). Exceptions are Transfrontier Conservation Areas, which connect reserves across international boundaries (Hanks 2003). Nonetheless, since many species have at least a part of their distribution in semi-natural habitats, such as those amongst agricultural and urban areas, these habitats have the potential to provide invaluable links between reserves and thereby to greatly enhance long term conservation success (Bush 1997, Farina 2000, Goodman 2003, Gaston & Spicer 2004, Dudley *et al.* 2005).

Successful conservation in human-influenced areas has many benefits (Duelli & Obrist 2003, Perrings *et al.* 2006), such as reducing erosion, benefiting hydrological processes and improving biological control of pest species (Kemper *et al.* 1999, Rieux *et al.* 1999, Speight *et al.* 1999, Tscharntke *et al.* 2002, Alkorta *et al.* 2003), by supporting and enhancing predators and parasitoid populations which prevent large pest outbreaks (Booij & Noorlander 1992, Bommarco & Ekbom 2000). Most importantly these areas potentially provide a natural reservoir of biodiversity from which disturbed areas can be restored (Kemper *et al.* 1999). Natural remnants in agricultural lands are therefore economically important (Kemper *et al.* 1999) and essential to both the long-term sustainability of agricultural production systems and biodiversity (Saunders *et al.* 1991, Bestelmeyer & Wiens 1996, Kemper *et al.* 1999, McGeoch 2002, Major *et al.* 2003).

Successful conservation in human-influenced areas requires knowledge of processes that drive and determine biodiversity in these areas (Parker & Nally 2002). Habitat loss and fragmentation of the remaining habitat (Saunders *et al.* 1991, Ovaskainen & Hanski 2003) as well as other habitat disturbances, such as livestock grazing, pesticides, invasion of foreign species, hydrological changes, changes in fire regimes, and pollutant effects such as acid rain are processes which characterize human-influences landscapes (Laurance & Cochrane 2001). These processes may act synergistically (McIntyre & Hobbs 1999, Laurance & Cochrane 2001) leading to a degradation of ecosystems, modifying the composition, structure and functioning of communities (Saunders *et al.* 1991). Although processes in human-influenced areas influence species negatively, many are nonetheless able to persist in these areas. This may however be due to a time delay in their response to the changing environmental conditions, a phenomenon known as extinction debt (Tilman *et al.* 1994). If

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environmental conditions fall below a threshold required by species for their long term survival, a "debt" is created, which has to be "paid" either by an improvement in environmental conditions or an extinction of the species (Hanski & Ovaskainen 2002). Extinction debt information is important for determining what is required in these areas to allow for long-term persistence of species and to develop effective management strategies to maximize biodiversity. However this information is currently unknown. Furthermore, for effective conservation of human-influenced areas, information on how observed patterns change with spatial scales is also important. Ecological patterns and processes are known to be strongly scale dependent, with patterns observed at local scales being quite different to those observed at regional scale (Lennon *et al.* 2001, Crist *et al.* 2003). Additionally, both regional and local-scale processes may generate local scale patterns (Noda 2004). Determining which spatial scale is responsible for generating the greatest variability in biodiversity is important for effective management and conservation strategies (Boyero 2003, Gering *et al.* 2003) and has received great emphasis recently (Wagner *et al.* 2000, Crist *et al.* 2003, Gering *et al.* 2003, Tylianakis *et al.* 2006). An example is a study of arboreal beetles in the eastern deciduous forest of the USA conducted by Gering *et al.* (2003), which found that species richness turnover between ecoregions as well as sites was significantly higher than expected by randomly allocating sites to the ecoregions and stands to sites respectively. From this they could deduce that the most effective way of preserving beetle diversity in this region is to protect multiple sites in different ecoregions, rather than investing effort in local-scale management approaches that strive to increase tree diversity within stands.

Although the importance of these natural remnants to conservation is well known in theory and many studies have emphasized the importance and role of human-influenced areas in conservation strategies (Samways *et al.* 1997, Kemper *et al.* 1999, Whitmore *et al.* 2002), in practice they are still poorly understood and the magnitude of the contribution that they play in regional biodiversity conservation is currently unknown. The broad aim of this study was therefore to determine the current contribution of natural remnants in human-influenced areas to conservation.

The study area

A region that lends itself to determine the conservation contribution of human-influence landscapes is the Cape Floristic Region (CFR). The CFR is a major biodiversity hotspot of global significance (Myers *et al.* 2000, van Wyk & Smith 2001, Cowling *et al.* 2003). Situated on the southern tip of Africa, covering an area of 90 000 km^2, this region has a high concentration of endemic taxons, particularly plants (around 70 %) (van Wyk & Smith 2001, Goldblatt & Manning 2002). Although plant species richness within an area at local scale is not very high compared to some other areas of the world, beta diversity in the CFR is exceptionally high (Goldblatt & Manning 2002). The region is however extensively transformed, currently 30 % of the total area, and continues to be increasingly threatened by factors such as urban development, (currently transforming 1.6 % of the area), agriculture (25.9 %) and dense stands of alien plant invasions (1.6 %) (van Wyk & Smith 2001, Rouget et al. 2003). Other contributing factors, which are less easily defined, are unsustainable harvesting of natural resources, such as wild flowers and mining and quarrying activities as well as poor grazing practices (van Wyk & Smith 2001, Rouget *et al.* 2003). Transformation of the region is however not evenly spread across the CFR, with low-lying mesic areas having received the greatest impacts (more than 90 % is transformed). In areas such as Sand Plain Fynbos, more than 50 % has been lost due to urbanization and less than 20 % of Coastal Renosterveld remains due to the impacts of agriculture (Rouget *et al.* 2003). Protected areas in contrast are focused on higher lying areas, with up to 90 % of mountain fynbos protected in nature reserves and mountain catchment areas, however less than 3 % of the easier accessible lowland fynbos and renosterveld are formally protected (van Wyk & Smith 2001). It is thus clear that in low-lying areas, available habitat is less than is required for any long-term conservation target (Rouget *et al.* 2003). High land values in most parts of the CFR along with high fragmentation makes establishment of new formal reserves mostly unachievable (Fairbanks *et al.* 2004). Hence involving landowners, especially farmers outside of protected areas to manage and protect remnants of natural or semi-natural vegetation on their land, is an important alternative or perhaps even the only option for achieving conservation targets for low lying regions of the CFR (Kemper *et al.* 1999, Cowling *et al.* 2003, Fairbanks *et al.* 2004).

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The taxa

Although the plant diversity of the CFR is well studied, comparatively little is known about the arthropod assemblages (Picker & Samways 1996, Visser *et al.* 1999, Giliomee 2003). It has been thought that insect diversity in the CFR is especially low in comparison to the rich plant diversity (Giliomee 2003). However a recent study showed that this is not the case, with arboreal insect species in the CFR being no less diverse than that of neighbouring biomes or what could be expected in insect diversity at that particular latitude (Proches & Cowling 2006). Arthropods are an integral part of ecosystems as their abundance and biomass dominate the biodiversity in most areas of the world (Major *et al.* 2003). They regulate many essential ecosystem processes, such as maintaining plant community composition, improving soil structure, nutrient cycling, pollination, seed dispersal and preying on other animals, thereby keeping their populations under control (Majer & Nichols 1998). Arthropods are also in general sensitive to disturbances (Madden & Fox 1997, Bolger *et al.* 2000, Witt & Samways 2004), however in the CFR little is known about their response to disturbances (Picker & Samways 1996, Donaldson *et al.* 2003, Major *et al.* 2003). Arthropods play a vital role in the CFR, where for example, ants (Formicidae) are responsible for dispersing seeds of more than 20 % of the plants in the region (Bond & Slingsby 1983) or seeds of more than 1300 taxa (Johnson 1992). For this reason and also due to their high abundance, ants were used as a target taxon. Ants are well studied in many areas of the world and frequently used as indicators in studies assessing impacts of management practices, habitat disturbances and rehabilitation successes (Andersen 1990, Majer & Kock 1992, Lobry DeBruyn 1993, Bestelmeyer & Wiens 1996, Samways *et al.* 1996, Samways *et al.* 1997, Majer & Nichols 1998, Peck *et al.* 1998, Bestelmeyer & Wiens 2001, French & Major 2001, Andersen *et al.* 2002, Perfecto & Vandermeer 2002, Hoffmann & Andersen 2003, Armbrecht *et al.* 2005, Bestelmeyer 2005, Underwood & Fisher 2006). Thus determining changes in ant assemblages could provide valuable information as to the contribution that remnants are able to make to conservation of the CFR.

Objectives and thesis outline

Research in biodiversity conservation is typically a crisis science, needing reliable answers faster than in-depth studies can provide them (Parr & Chown 2001). Hence rapid assessment protocols are important as they seek to optimize the sampling effort (in terms of person power, time and finances) and the reliability and representivity of the samples collected (Jones & Eggleton 2000, Parr & Chown 2001, Leponce *et al.* 2004). Typically invertebrate studies involve large sampling effort (Andersen *et al.* 2004) and hence an initial step was to determine an optimal sampling effort for arthropods in the CFR, this was done in Chapter 2. To determine the reliability of a "snap-shot" view of a single sample, in representing broader arthropod assemblage patterns across the year, seasonal sampling was conducted in a single area and the outcome of this study is reported in Chapter 3. This base-line information is important not only for this study, but also in general since there is very little seasonal information available on ants or other ground-dwelling arthropods in the CFR. Finally in Chapter 4 the current contribution of remnants in human-influenced areas of the CFR to the overall conservation of the CFR was determined, using ground-foraging ants as a target taxon. Additionally the spatial scale which contributes most to generating ant diversity in the CFR was also determined (Chapter 4). Chapters in this thesis were written as individual manuscripts and there is thus some repetition. Finally a general conclusion (Chapter 5) provides a brief summary of the main findings of this study and their contribution to the broader theoretical and conservation arena.

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FINE SCALE TEMPORAL AND SPATIAL DYNAMICS OF EPIGAEIC ANTS IN FYNBOS: SAMPLING IMPLICATIONS

INTRODUCTION

A fundamental element of conservation and biodiversity management is information on species richness, i.e. the number of species in a unit area or assemblage (Gotelli & Colwell 2001, Cao *et al.* 2004, Magurran 2004). Although biodiversity can be measured in a variety of ways, the most commonly used is species richness (Lande 1996, Arita & Rodrígues 2002, Gaston & Spicer 2004). Reasons for this are that species richness is a relatively practical and simple measure to take in the field (Lande 1996, Gaston & Spicer 2004). Also, vast amounts of species richness information can be found in the literature and in museums (Gaston & Spicer 2004). Additionally, as a measure, species richness is widely used by managers, legislators and politicians, who often inadvertently equate biodiversity to species richness (Buchs 2003, Gaston & Spicer 2004). Species richness estimates across time and space can also be used to determine other measures underlying conservation strategies, such as species turnover rates, species extinction and colonization (Cao *et al.* 2004). Species richness and evenness values are also commonly employed to compare sites and to assess their conservation value, as well as to determine the effects of disturbances, human or natural, on biodiversity (Longino 2000, Cao *et al.* 2004, Colwell *et al.* 2004).

Information on species richness is especially valuable for helping to prioritize specific areas for conservation efforts in regions which are highly diverse and threatened by factors such as habitat destruction, invasive species and climate change (Rodrigues & Gaston 2002, Rouget *et al.* 2003, Cao *et al.* 2004, Magurran 2004, Opdam & Wascher 2004). One such area is the Cape Floristic Region (CFR), South Africa, which is considered a global biodiversity hotspot (Myers *et al.* 2000). Although much is known about plant species richness in the region (Cowling & Hilton-Taylor 1994), insect diversity is relatively poorly understood (Giliomee 2003). Arthropods are, however, critically important in the region, functioning, amongst others, as pollinators, seed dispersers and natural predators (Donaldson *et al.* 2003, Giliomee 2003, Witt & Samways 2004), and arthropod diversity information is therefore invaluable for the conservation of biodiversity in the region.

However, to ensure confidence in conservation decisions and to meaningfully compare sites, species richness counts need to be accurate (Gotelli & Colwell 2001). Although, species richness is the oldest and simplest measure used to describe biodiversity, it is notoriously difficult to obtain an accurate measure of it, particularly for arthropods (Colwell & Coddington 1994, Magurran 2004). Reasons for this are that assemblages are often very diverse and a large sampling effort is required to represent all species (Magurran 2004). Also, assemblages frequently have a high proportion of rare species, which are underrepresented in samples (Gotelli & Colwell 2001, Magurran 2004). Additionally, high levels of temporal heterogeneity (e.g. seasonal variation) especially in invertebrates can result in seasonal specialist not being trapped (Magurran 2004). Finally, a high local heterogeneity in some areas, to the extent that two areas within the same habitat type at a local scale are significantly different in terms of the assemblage structure for a given taxon, can lead to inaccurate species richness measures (Gotelli & Colwell 2001).

Due to the problems associated with obtaining accurate species richness measures, techniques have been developed that provide comparable richness estimates with quantified degrees of certainty for situations where sample representivity is insufficient (Cao *et al.* 2004, Chao *et al.* 2005). These species richness estimators thus provide comparable richness estimates where sample effort across sites is unequal or insufficient (Colwell & Coddington 1994). Nonetheless, sampling diverse assemblages with low evenness values, such as arthropod assemblages, requires large sampling effort which is highly resource intensive in terms of person power, finances and time (Colwell & Coddington 1994, Sutherland 1996, Longino 2000, Colwell *et al.* 2004). At the same time large samples result in collection of more material than necessary, which is not only time-consuming to sort, but also unethical (New 1998, Jones & Eggleton 2000). Hence, there are several important advantages to optimizing sampling effort such that maximum sampling representivity is achieved with minimum sampling effort.

Most studies that aim to quantify the species richness and composition of a region rely on taxon-appropriate sampling methods replicated within that particular region. In addition, biodiversity estimate studies, due to time constraints, commonly sample on a single occasion, where the timing of the sample coincides with the peak activity period of the taxon of interest (Davis *et al.* 1999, van Rensburg *et al.* 1999,

McGeoch *et al.* 2002). This study therefore aimed to determine the optimal sampling effort in a given season, for a given taxon in the CFR, namely ants (Formicidae).

Ants form an important component of the fauna of the CFR and fulfill a critical role as seed dispersers for more than 20 % of the plant species in the region (Johnson 1992). The most widely used and standard method for trapping ground-foraging ants is pitfall-trapping (Andersen 1986, Lobry DeBruyn 1993, Southwood & Hendersen 2000, Parr & Chown 2001). Although this method is know to have biases in estimating population parameters (Samways *et al.* 1996, Bestelmeyer *et al.* 2000, James 2004), it is nonetheless reliable for trapping epigaeic fauna and useful for comparative studies (Samways 1990, Southwood & Hendersen 2000). Increasing sampling effort using pitfall trapping includes an increase in sampling intensity or an increase in trapping duration (Delabie *et al.* 2000, Brown *et al.* 2004, James 2004). An increase in sampling intensity can be brought about by increasing the sampling coverage (proportion of sampling extent represented) and/or the sample number within the extent of a given grain size, as sampling intensity is given by the product of these two (McGeoch & Gaston 2002). Increased duration generally involves leaving the traps open for longer periods of time, or temporal repetition of trapping. Both of these measures increase sampling effort and have been demonstrated to increase the number of, especially rare, species captured (Sutherland 1996, James 2004).

This study thus investigated sampling effort options for maximizing gound-foraging ant species representivity, i.e. obtaining a species list that is representative of the ants in the area, when sampling a component of the CFR, namely the lowland fynbos biome. The aims were to determine, i) whether doubling the sampling duration results in a significant increase in species richness, ii) the relative effects of increased spatial versus temporal sampling effort on diversity estimates and iii) what the effect of an additional trapping method, in this case tuna baiting, is on the species richness obtained.

MATERIAL AND METHODS

Study site and sample design

This study took place on Elandsberg Private Nature Reserve (33.27° S, 19.03° E) and surrounding Bartholomeus Klip Farm, near Hermon, Western Cape Province. The reserve, lying at the foothills of the Elandskloof Mountain range, was proclaimed

in 1973 and encompasses approximately 3600 of the 5000 ha Farm (Midoko-Iponga 2004). The surrounding farmlands include wheat fields, and cattle and sheep grazed areas. Elandsberg has two main vegetation types, namely Swartland Alluvium Fynbos and Swartland Shale Renosterveld, both of which are critically endangered (Mucina & Rutherford 2004). Elandsberg receives a mean annual rainfall of about 500 mm.

The sample design used consisted of 10 grids, each containing 10 pitfall traps spaced 10 m apart in two rows (2 x 5). The position of each grid was randomly chosen and marked using a Garmin GPS. Sites were chosen to represent the Elandsberg area, including the reserve and natural remnants scattered between wheat fields (Fig. 1). Four of the grids were situated in Swartland Alluvium Fynbos-dominated vegetation and another in Swartland Shale Renosterveld-dominated vegetation. Two grids fell on road and field side verges with relatively intact natural vegetation remaining, although cattle were allowed to graze the area. A further two grids were on old fields with limited natural vegetation and the final one was in a vlei area surrounded by wheat fields with relatively rich plant species diversity. All grids were between altitudes of 71 - 170 m.a.s.l. and were placed between 200 and 250 m apart.

Sampling

Sampling was conducted in summer between 20 February and 1 March 2004, as this time has been recorded to include the peak activity period for ants in the Cape Floristic Region (Johnson 1992). The pitfalls used were plastic containers (150 ml, 55 mm diameter, 70 mm deep) with screw-on caps. These were dug in level with the surrounding soil surface. The pitfalls remained covered for the first five days, to reduce the digging-in effect (Greenslade 1973, Abensperg-Traun & Steven 1995, Southwood & Hendersen 2000), after which they were opened for a period of five days per sampling event. To set the traps, 50 ml of 50 % propylene glycol solution was poured into the opened pitfalls (Bestelmeyer *et al.* 2000). This preservative is non-toxic to vertebrates (Bestelmeyer *et al.* 2000), and neither attracts or repels ants (Abensperg-Traun & Steven 1995). After the first sampling period of five days, pitfalls were carefully removed and new pitfalls were inserted into the same holes and reset. Pitfalls were set and removed in the same order over as short a period as possible, typically between 10h00-15h00, to ensure that they were open for equal lengths of time. The contents of the pitfalls were washed by pouring it into a net and

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gently rinsing off the loose soil and propylene glycol with water. The remaining content was then preserved in 70 % alcohol.

Baiting was used as an additional sampling technique for ants. Tuna baiting was used, as this is the most commonly used food substance to attract ants (Bestelmeyer *et al*. 2000), see also Addison & Samways (2000). One teaspoon of shredded, tinned tuna was placed 20 – 30 cm from a pitfall trap in each grid. This was done after the first sampling period pitfalls had been removed and new ones had just been inserted. The baits were left for 45-60 min between 10h00 and 15h00 (leaving baits for longer does not increase the number of species found (Delabie *et al.* 2000)), after which all ants feeding on the tuna were collected and placed in 70 % ethanol.

The fauna of both pitfall traps and tuna baiting were identified under a Leica-M Series Stereo-microscope. The ants (Hymenoptera: Formicidae) were identified to genus and species level where possible, or assigned morphospecies using Bolton (1994) and Hölldobler & Wilson (1990). For each species collected voucher specimens are held at the University of Stellenbosch.

Data analyses

All pitfall data were analysed at the grid level (n = 10). To estimate sampling representivity (Gotelli & Colwell 2001), rarefaction curves were compiled separately for the first five days, second five day and full 10 day data sets using EstimateS V7, R.K. Colwell 2005, http://viceroy.eeb.uconn.edu/estimates. Species rank abundance curves were constructed (Magurran 2004) to compare the rank abundance distributions of the first and second trapping periods.

To investigate the effects of the three sampling options, data were subdivided into different categories: 1. To investigate the effects of increased sampling duration, pitfall data were divided into first five days, second five days and a combined first plus second trapping period (10 day sampling period), using all 10 grids data. 2. The effects of the increase in sampling intensity was investigated using the mean of five randomly chosen grids (5 grids were randomly chosen 1000 times) and comparing it to that of the full 10 grid data set, using only the first five days trapping period data. To compare the effects of increased sampling duration and intensity, rarefaction curves were compiled using sample-based rarefaction curves (Gotelli & Colwell 2001). Sample-based rarefaction curves, also known as expected accumulation curves, were compiled using the analytically calculated S_{obs} (Mao Tao) of EstimateS, which

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does not require resampling methods (Colwell 2005). This was done for the first five, second five and full 10 day sampling period data sets. Note that due to the way in which rarefaction curves are calculated, the mean of the randomly chosen five grid data as well as that of the full 10 grid data, for the first five days, are given by the first five day curve. Sample-based rarefaction curves were used to compare data sets on the basis of species density, i.e. number of species per unit area (Gotelli & Colwell 2001). To compare species richness for a given number of individuals, sample-based rarefaction curves must be standardized by the number of individuals (Gotelli & Colwell 2001), and hence S_{obs} was plotted against calculated number of individuals for species richness comparisons.

Additionally, a spatially constrained curve for the total data set was generated manually using the full 10 day data set, to investigate the effect of spatial autocorrelation on the rarefaction curves. This was done by starting at a randomly selected grid (for example A) and then determining the cumulative number of species for the nearest neighbouring grid (for example C), determined from the map of the GPS coordinates (Fig. 1), followed by the next nearest grid and so on. The process was repeated starting at each of the 10 grids in turn. The mean values for each of the 10 grid runs were then used to construct the curve. The shapes of the rarefaction curves were compared visually with that of the spatially constrained model. To formally test for the presence of spatial autocorrelation in richness and abundance, SAAP v 4.3 and Moran's I were used (Wartenberg 1989).

To estimate the total (*sensu* Hortal *et al.* 2006) ant species richness for Elandsberg, a series of non-parametric species estimators, provided by EstimateS, was used. This approach was used because observed species richness obtained from sampling is considered to provide a biased estimate of total richness (Colwell & Coddington 1994). Determining which of these estimators is least bias and most accurate and precise for the specific set of data is complex, and dependent on factors such as community evenness and sampling intensity (Brose *et al.* 2003). Colwell & Coddington (1994) suggest that Chao 2 and Jack 2 (Jacknife 2) perform best for small sample sizes. Michaelis-Menten and incidence-based coverage estimator (ICE) are two additional estimators that perform well for small samples sizes (Magurran 2004). Since datasets differed in their underlying species abundance distributions and, therefore, influenced the performance of different estimators in different ways, all four of the above estimators were used for comparison (Brose *et al.* 2003). Species

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richness estimators were calculated using 1000 randomisations, with sample replacement. Although randomisation without replacement provides a more accurate species richness estimate, for statistical comparison purposes using sample replacement gives variances for the full number of samples (Colwell 2005). The ICE values were then also used in z-tests to determine significant differences between five and ten days (both using 10 grids) and also five grids and ten grids (using 10 days). The tuna baiting data are summarized as a footnote in the appendix, and were excluded from all the above analyses.

RESULTS

A total of 8207 individuals, comprising five genera and 42 species were captured in total across all grids over the 10 day sampling period (Appendix A). The first and second trapping periods both yielded 38 species, with four species not shared between the two. However, the second five day sampling period yielded fewer individuals than the first (Appendix A). The highest species richness for a grid was 18 and the lowest was 6 species. Approximate asymptotes to species richness were reached (Fig. 2). Estimates of total species richness ranged between 43.55 ± 4.04 (ICE) and 48.52 (MMMean) (Table 1). All four species richness estimators showed similar trends for species richness across the sampling options, with the first five days having a marginally lower species richness estimate than the second five days (Table 1).

The species captured in the first trapping period showed a clear dominance structure, with *Pheidole* sp.1 being most abundant (Fig. 2). The relative abundance distribution in the second trapping period was similar to the first, although *Pheidole* sp.1 and *Anoplolepis steingroeveri* (Forel) were both equally dominant. In the first five and second five trapping days, 26 and 27 species respectively had a relative abundance of less than one percent.

Species accumulated more rapidly across samples in the first trapping period than in the second period (Fig. 3A). However, more species were found per individual for the second compared to the first trapping period (Fig. 3B). For an increase in sampling duration (5 days vs 10 days), species richness increased from 38 to 42 species (or an estimated 4.1 species increase using ICE) (Table 1), which was a non-significant increase ($z = -1.50$, p (one tailed) $= 0.067$). An increase from one randomly

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selected set of five grids to 10 grids using all 10 days showed an estimated 10.72 species increase (using ICE), which was significant (z = -3.88, p (one tailed) = 0.001).

Comparing sampling effort options, Fig. 4 shows that increasing effort from a mean five-day, five-grid pitfall sample leads to an almost identical increase in species richness for both sampling intensity (spatial, 38 species) and duration (temporal, 38.3 species). However, species turnover, or the number of species not shared between replicates was lower for temporal (1st 5 days and 2nd 5 days) than for spatial (5 randomly selected grids and 5 remaining grids) replicates (Fig. 5). Most of the species that were found in only one replicate were also rare in the overall sampling (Appendix A). Results of the spatial autocorrelation analysis, using Moran's I, showed that species richness and abundances of sites closer together were not more similar than would be expected by chance, as the correlograms (for each species in each period and in total) were non-significant (p > 0.05 in all cases). The third sampling option, tuna baiting, added no new species to those already caught in pitfall traps (Appendix A).

DISCUSSION

This study investigated three different sampling options for increasing and ultimately maximizing sampling representivity of the ant assemblage in a low-lying area of the CFR. The results show that, at this local site scale, increases in sampling effort in terms of increasing the sampling duration and sampling intensity (number of sampling units in an extent) result in a similar increase in ant species richness captured. Thus both sampling options appear to be equally effective for measuring species richness. However, species shared between spatial replicates was much lower than that between temporal replicates, indicating a higher turnover between spatial replicates compared to temporal ones.

Species richness of ants at Elandsberg was similar to that of other studies conducted in the CFR using pitfall trapping. Across 14 sites in the CFR moderately infested with *Acacia saligna*, 47 Formicidae species were found, using 10 pitfalls per site, 5 m apart, left open for 7 days (French & Major 2001). In the Proteoid Fynbos of the Cederberg, using a pitfall sampling design much like the one used in this study with sampling being representative of the area, 47 species were found (Botes *et al.* 2006). In the Jonkershoek Valley, 45 species were captured across six sites using 20

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pitfalls per site which were left open for 1 month in 24 hour intervals (Donnelly & Giliomee 1985). The sampling conducted in this study is thus considered effective as a means of estimating the local species richness of Formicidae. Sampling during spring may result in higher species richness for Elandsberg, however species richness of samples was nonetheless typical for the CFR and hence sampling can be considered to approximate total species richness for the area.

Comparing the two consecutive five-day trapping periods, more individuals were captured during the first trapping period than in the second trapping period. However the number of species was the same for both trapping periods, therefore resulting in species accumulating faster per number of individuals for the second trapping period compared to the first. Also, the second trapping period had many more species caught in only one grid, i.e. more unique species. The reason for lower numbers of individuals during the second period may be a trapping-out effect (Bestelmeyer *et al.* 2000). However, the cooler weather conditions (a low of 11°C and rain on one day) during the second trapping period, which is likely to have reduced ant foraging activity, is more likely (Andersen 1997, Bestelmeyer *et al.* 2000). The first trapping period, by contrast, had temperatures greater than 30°C, favouring thermophilic species such as *Ocymyrmex* species (Hölldobler & Wilson 1990).

Comparing the rarefaction curves of the 5 *versus* 10 grids (using the 1st 5 days data) and 1st 5 days and 10 days (using 5 grids) permitted a direct comparison of the effect of a doubling in sampling duration with that of doubling in spatial replicates. The results showed an equal increase in species richness for both sampling options, but a greater number of species were replaced between spatial replicates than between temporal replicates. This turnover was greater than could be explained by spatial autocorrelation alone, as the latter analysis was non-significant. This was also apparent in the spatially constrained model's curve, where species accumulated more rapidly in the rarefaction curves than the spatially constrained model predicted. Hence the spatial turnover in species was apparently determined more by habitat heterogeneity than by spatial autocorrelation.

The greater species turnover between spatial replicates compared to temporal replicates indicates that if sampling efforts in this area were to be increased further, increasing spatial replicates is likely to be more effective than relative increases in the number of sampling days within a season. A study aimed at comparing various methods and sampling efforts for collecting ants in the Brazilian cocoa plantations,

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supports this idea. In this study, increasing the sampling duration from 24 hours to 7 days, for 10 samples, lead to a 0.6 % increase in the total estimated species richness captured. However increasing the number of samples over a 7 day period, from 10 to 20 and 40 lead to a 15.2 % and 35.9 % increase in total estimated species richness respectively (Delabie *et al.* 2000). This suggests that our finding applies more generally.

The third technique, implementing an additional collecting technique, although recommended when sampling invertebrate assemblages (New 1998, Bestelmeyer *et al.* 2000), did not trap any new species. This has also been found in a previous study in the CFR where various baits, including banana/rum mixture, rotten pork and human faeces were found to be ineffective for trapping additional species (Koen & Breytenbach 1988). Reasons for tuna baiting being ineffective could be due to the tendency of baits to be monopolized by mass-recruiting dominant species (Bestelmeyer *et al.* 2000), which are then already present in pitfall traps. Leaving baits out for a shorter time period such as 5 - 15 min, could limit species dominating baits. Baiting is nonetheless useful for studying ant behaviour (Bestelmeyer *et al.* 2000), but since we were interested in gaining species richness estimates, tuna-baits were not a successful additional method to use with pitfall trapping.

It is important to note that this study was not aimed at catching all the species at the site, but rather at maximising richness for a set effort. In order to obtain a complete estimate of the species richness of an area sampling would have to be conducted throughout the year (New 1998, James 2004). This would ensure that species that are highly seasonal would also be captured (New 1998, Delabie *et al.* 2000, Magurran 2004). However due to time constraints and limited resources, species richness measures in comparative studies are most often obtained using a single sampling period and trapping method (McGeoch *et al.* 2002).

In conclusion this study shows that sampling efforts of ants in the CFR are maximised by increasing the spatial sampling intensity rather than increasing sample duration. Therefore, it is more beneficial to sample using more grids than to sample over a longer time interval. Studies such as this are important for increasing the efficiency of sampling.

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Table 1 Ant species richness, number of individuals, number of species found only in one grid, and species richness estimates based on incidence-based coverage estimator (ICE), Chao 2, Jackknife 2 and Michaelis Menton Mean (MMMean).

	1st five days	2nd five days	Total
Observed species richness (S)	38	38	42
Number of individuals	5065	3142	8207
Number of unique species	4 ± 3.57	5.52 ± 4.56	4.48 ± 4.1
Species richness estimators ± sd			
ICE	39.44 ± 3.46	40.59 ± 6.07	43.55 ± 4.04
Chao 2	39.25 ± 3.56	40.92 ± 6.07	46.01 ± 4.37
Jackknife 2	39.41 ± 6.56	39.98 ± 9.1	43.71 ± 7.91
MMMean	43.67	45.64	48.52
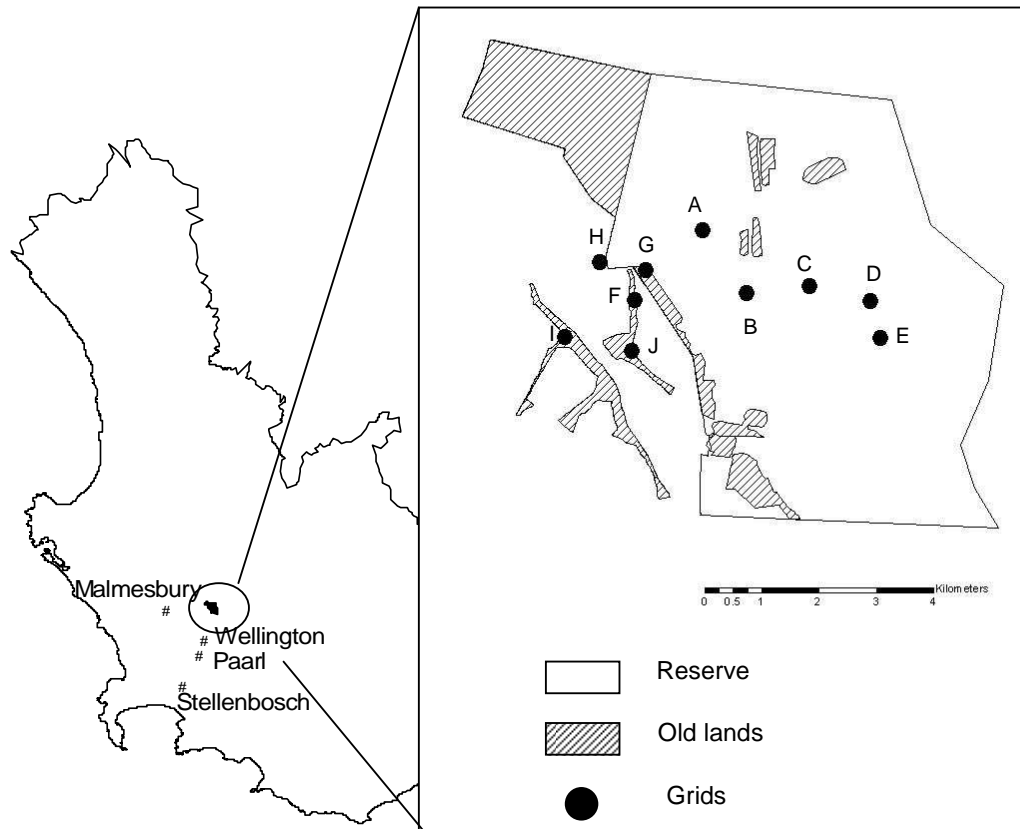
Figure 1 Map showing study grids at Elandsberg, Western Cape Province, South Africa.
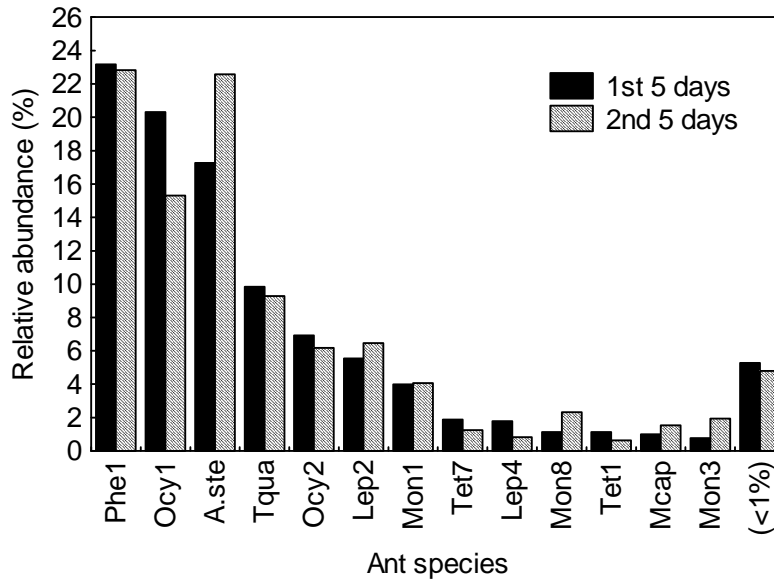
Figure 2 Formicidae species rank abundance bar charts for two consecutive 5 - day periods. Phe1 = *Pheidole* sp.1, Ocy1, 2 = *Ocymyrmex* sp.1, 2, A.ste = *Anoplolepis steingroeveri*, Tqua = *Tetramorium quadrispinosum*, Tet7, 1, = *Tetramorium* sp. 7, 1, Lep2, 4 = *Lepisiota* sp.2, 4, Mon1, 8, 3 = *Monomorium* sp.1, 8, 3, Mcap = *Messor* capensis. The species which had a relative abundance less than 1 % for both trapping periods were summed and given in the last column (< 1 %).

A

B
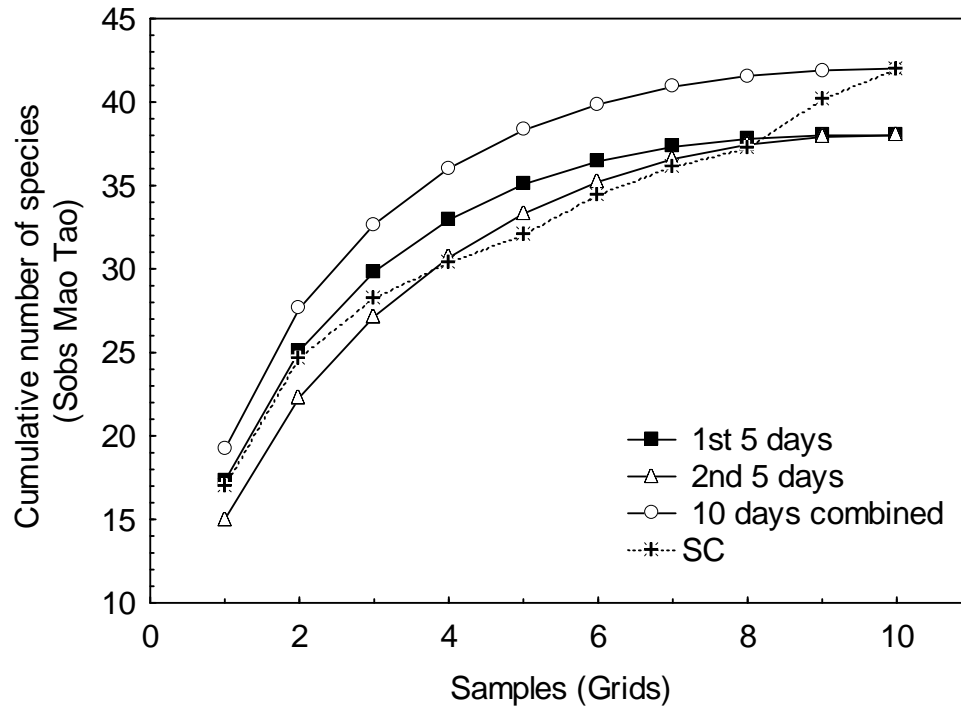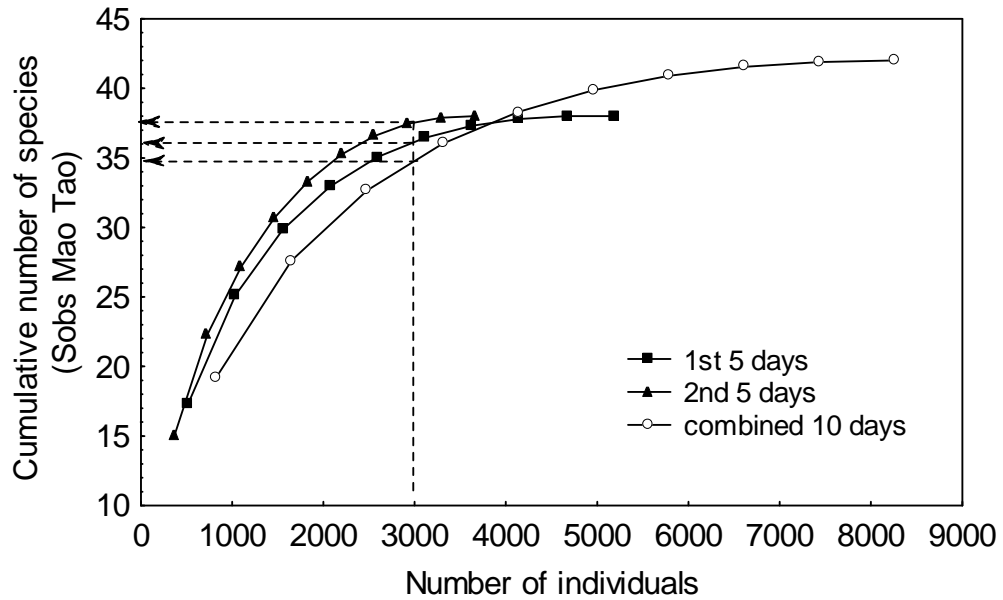
Figure 3 Sample-based rarefaction curves for ant pitfall catches at Elandsberg over two consecutive 5-day periods, using S_{obs} (Mao Tao) (**A**) and samples and (**B**) individual. SC is a spatially constrained model that was generated manually.

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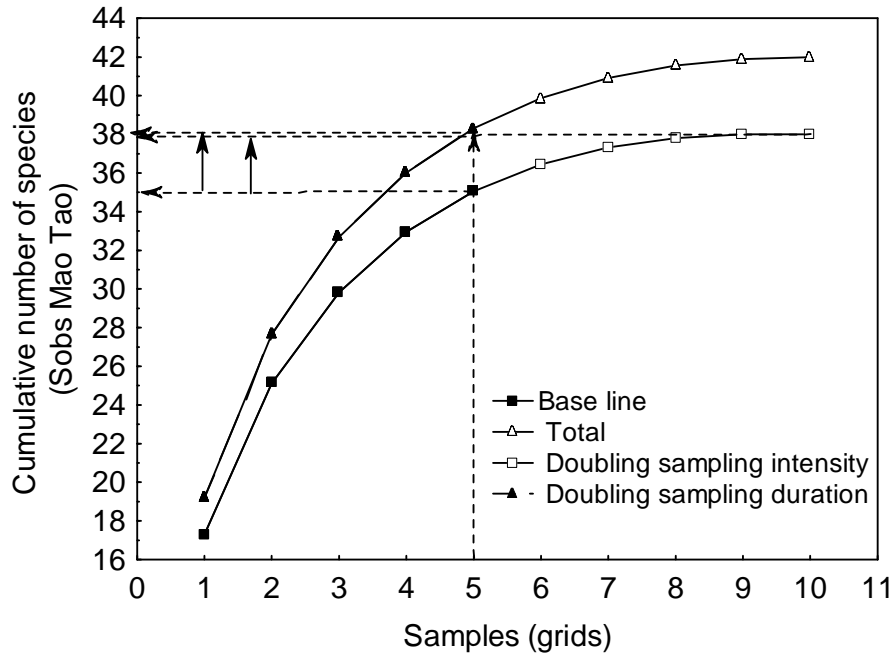
Figure 4 Sample-based rarefaction curves showing the effects of increased sampling intensity and increased sampling duration of Formicidae pitfall catches. Base line = sampling for 5 days using 5 grids. Doubling sampling intensity = sampling for 5 days using 10 grids. Doubling sampling intensity = sampling for 10 days using 5 grids and total = sampling for 10 days using 10 grids.
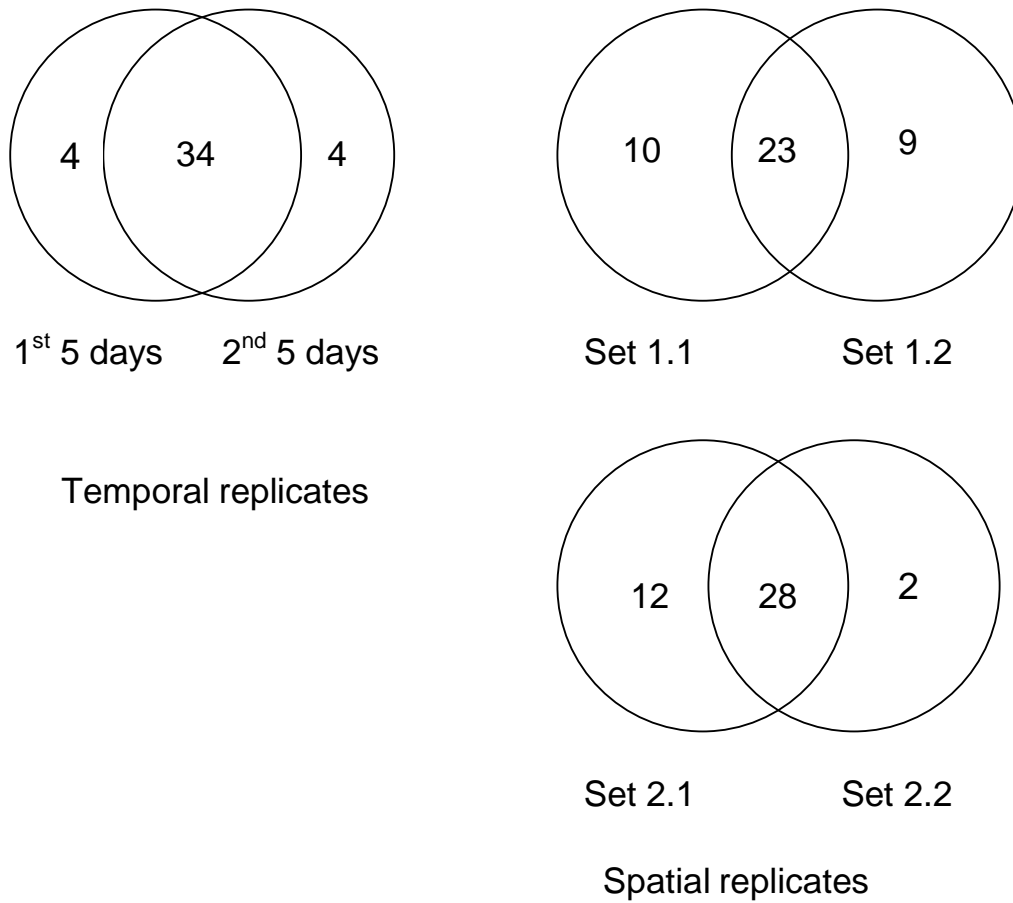
Figure 5 Number of unique (outer half circles) and shared (area of overlap) Formicidae species for one temporally replicated set and two spatially replicated sets. Spatial replicates were obtained by a random selection of 5 grids and the remaining 5 were then used as the complement per set, i.e. 1.1 and 1.2.

APPENDIX

Appendix A. Formicidae species and number of individuals collected using pitfall traps at Elandsberg over a 10 day period. Symbols ***** = only present in 1st 5 days, ° = only present in 2nd 5 days.

| Species	1st 5 days	2nd 5 days	Total
Dolichoderinae			
Technomyrmex sp. 1 *	5	0	5
Dorylinae			
Dorylus helvolus (Linneaus) °	0	1	1
Formicinae			
Anoplolepis steingroeveri (Forel)	874	709	1583[1]
Anoplolepis sp.1	18	2	20
Anoplolepis sp. 3	4	6	10
Camponotus fulvopilosus (DeGeer)	7	2	9
Camponotus sp. 1	6	4	10
Camponotus sp. 2	4	6	10[2]
Camponotus vestitus (F. Smith)	15	21	36
Camponotus mystaceus (Emery) °	0	2	2
Camponotus sp. 5	2	1	3
Camponotus sp. 6	1	1	2
Lepisiota sp. 2	281	203	484
Lepisiota sp. 3	12	1	13
Lepisiota sp. 4	90	26	116
Lepisiota sp. 5	12	18	30
Myrmicinae			
Crematogaster sp. 1	20	3	23
Messor sp. 1	18	11	29
Messor capensis (Mayr)	51	48	99
Monomorium sp. 1	202	128	330
Monomorium sp. 2 *	3	0	4
Monomorium sp. 3	39	61	100
Monomorium sp. 4	1	3	4

Monomorium sp. 5 *	13	0	13
Monomorium havilandi (Forel) °	0	1	1
Monomorium sp. 7	38	23	61
Monomorium sp. 8	57	73	130
Ocymyrmex sp. 1	1029	481	1510[1]
Ocymyrmex sp. 2	351	194	545
Pheidole sp. 1	1173	717	1890[3]
Rhoptromyrmex sp. 1	6	2	8
Tetramorium sp.1	57	20	77
Tetramorium quadrispinosum (Emery)	499	292	7912
Tetramorium sp. 3	44	13	57
Tetramorium sp. 5	10	12	22
Tetramorium sp. 7	95	39	134
Tetramorium sp. 8	4	2	6
Tetramorium sp. 9	5	1	6
Tetramorium sp. 10 *	1	0	1
Cardiocondyla sp. 1 °	0	1	1
Ponerinae			
Anochetus levaillanti (Emery*)*	1	1	2
Pachycondyla sp. 1	17	13	30
Total	5065	3142	8207

[1] An additional 134 individuals were caught using tuna bait trapping

[2] One individual was caught using tuna baiting

[3] An additional 275 individuals were caught using tuna baiting

CHAPTER 3
SEASONAL CHANGES IN ARTHROPOD ASSEMBLAGES IN LOWLAND
FYNBOS OF THE CFR

INTRODUCTION

The Cape Floristic Region (CFR) has been listed as a biodiversity hotspot of global significance (Cowling *et al.* 2003). With over 9000 plant species occurring in this region, 70 % of which are endemic (van Wyk & Smith 2001, Goldblatt & Manning 2002) and 1406 Red Data Book plant species, this area boasts the greatest concentration of rare species in the world (Cowling & Hilton-Taylor 1994). The region is also an Endemic Bird Area as well as a centre of endemism and diversity for mammals, fish, amphibians, reptiles and many invertebrate groups (Picker & Samways 1996, Cowling *et al.* 2003). This region is however highly threatened by factors such as urban development, agriculture, dense stands of alien plant invasions, unsustainable harvesting of natural resources (such as wild flowers and mining and quarrying activities) as well as poor grazing practices (van Wyk & Smith 2001, Rouget *et al.* 2003). These transformations have been particularly severe in the lowlands (Rouget *et al.* 2003). Although, much is known about the plant diversity of the region, comparatively little is known about the arthropod assemblages (Picker & Samways 1996, Visser *et al.* 1999, Giliomee 2003). South African Museum records show 111 invertebrate species to be endemic to the Cape Peninsula, with the majority of the species living in upper-reach forest streams, riverine forest and caves (Picker & Samways 1996). However not much is known about the invertebrate diversity in other parts of the CFR and hence the possibility of finding many more endemic species exists (Picker & Samways 1996).

Arthropods are well known to play a crucial role in ecosystems and a change in their assemblages can potentially affect the entire ecosystem (Wilson 1987, Madden & Fox 1997, Bolger *et al.* 2000, Major *et al.* 2003). Functions performed by arthropods include pollination, seed dispersal, improving the soil structure, nutrient cycling, and control of pest species by arthropod predators (Bestelmeyer & Wiens 1996, Majer & Nichols 1998). Arthropods also perform vital functions in the CFR, where for example, ants are responsible for dispersing seeds of over 20 % of the plant species (Bond & Silingsby 1983). Hence determining base-line information on arthropods assemblages and their variability is of great value to the CFR.

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A prominent feature of assemblages is their variation in both time and space (Samways 1990). Arthropod species and their abundances are known to change, often dramatically, across seasons, because they are influenced directly or indirectly by changing weather conditions such as temperature, day-length, sunlight, precipitation and wind (New 1998, Speight *et al.* 1999). Mediterranean climates, such as that of the CFR, are characterized by large temperature and humidity fluctuations across seasons, as well as great variability in availability of food resources (Retana & Cerdá 2000, Stamou *et al.* 2004). These fluctuations are known to be mirrored by the arthropod assemblages (Retana & Cerdá 2000). However, in the CFR very few published studies have monitored seasonal changes in arthropod (Schlettwein & Giliomee 1987, Wright & Giliomee 1990, Visser *et al.* 1999, Wright & Samways 1999). The aim of this study was thus to quantify seasonal changes in ground-dwelling arthropod taxa, in a low–lying area of the CFR. Additionally, specific focus was placed on changes in ant (Hymenoptera: Formicidae) assemblages, because they are numerically dominant in ground dwelling assemblages in this region.

MATERIAL AND METHODS

Sample design

This study took place on the Elandsberg Private Nature Reserve (19.03° E, 33.27° S) and surrounding Bartholomeus Klip Farm, near Hermon in the Western Cape Province. The Reserve was proclaimed in 1973, and encompasses approximately 3900 of the 6500 ha farm (Midoko-Iponga 2004). The reserve lies at the foothills of the Elandskloof Mountain range and is surrounded in the lowlands by farmland, including wheat fields and cattle and sheep grazed areas. Elandsberg has two main vegetation types, Swartland Alluvium Fynbos and Swartland Shale Renosterveld, both of which are critically endangered (Mucina & Rutherford 2004). This reserve protects the largest remaining unploughed lowland area of these two vegetation types in the CFR.

The sample design used consisted of ten 20 x 50 m grids, five on the Elandsberg Private Nature Reserve and five on adjacent degraded remnants of lowland fynbos found between the farmlands (referred to as remnants from now on). The position of each grid was randomly determined and marked using a Garmin GPS (see Chapter 1, Fig.1). The remnants included two grids on road and field side verges with relatively

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intact natural vegetation remaining, although cattle were allowed to graze the area. A further two grids were on old fields, with limited natural vegetation. The fifth grid was in a vlei area surrounded by wheat fields with relatively rich plant species diversity. In the reserve, grids were also chosen to represent some of the heterogeneity of the vegetation, including a Swartland Shale Renosterveld vegetation dominated grid and four Swartland Alluvium Fynbos vegetation dominated grids. One of the reserve grids was situated inside a BIOTA Observatory. BIOTA is a long-term research project analysing biodiversity and its change along a transect in Namibia and the western parts of South Africa. Cooperative research is conducted on 35 standardized monitoring sites, BIOTA Observatories, by African as well as German scientists, with the goal of generating knowledge for effective maintenance and sustainable use for biodiversity (Schmiedel & Jürgens 2005).

All grids in this study were between 71 - 170 m.a.s.l. and were placed approximately 200 to 250 m apart. Sampling was conducted on four occasions during 2004: 20 - 25 February (late summer/autumn, referred to as autumn from now on), 2 - 7 June (winter), 6 - 11 October (spring) and 8 - 13 December (summer).

Weather data sampling

Weather data for Elandsberg were obtained from the Diemerskraal Weather Station, Paarl (33.35°S, 18.55°E). This included rainfall, maximum and minimum temperatures as well as relative humidity and mean wind speed. Data were provided by the AgroMet-ISCW Agricultural Research Council.

Vegetation Sampling

For each of the four sampling events, vegetation structure around each of the pitfalls (see arthropod sampling below) was sampled. To estimate the percentage vegetation cover, the following categories were used: bare soil, litter, grass, herbaceous component and woody plants. A square (1 m^2) was placed over each pitfall and then the percentage of each category in the square was estimated. Vegetation height profiles, also referred to as foliage height profiles (FHP), around each pitfall were also measured to determine the vertical density of the vegetation at different heights (Bestelmeyer & Wiens 1996). This was done by taking four measurements with a measuring rod. The rod was placed at four points located 90° apart on a 1 m radius circle with the centre at the pitfall. Measurements were divided

into 7 height classes of 0.25 m intervals, with plants above 1.50 m assigned to the last height class. All parts of the plant that touched the measuring pole within a certain height class were recorded (Bestelmeyer & Wiens 1996, Bestelmeyer *et al.* 2000).

Arthropod sampling

Pitfall sampling was used to trap ground-dwelling arthropods. The pitfalls used were plastic containers (150 ml, 55 mm diameter, 70 mm deep) with screw-on caps. These were dug in level with the surrounding soil surface. The pitfalls remained covered for the first five days to reduce the digging-in effect (Greenslade 1973, Abensperg-Traun & Steven 1995, Southwood & Hendersen 2000), after which they were opened for a period of five days per sampling event. To set the traps 50 ml of 50 % propylene glycol solution was poured into the opened pitfalls (Bestelmeyer *et al.* 2000). This preservative is non-toxic to vertebrates (Bestelmeyer *et al.* 2000), and neither attracts nor repels ants (Abensperg-Traun & Steven 1995). Pitfalls were set and removed in the same order over as short a period as possible, typically between 10h00-15h00, to ensure that they were open for equal lengths of time. Sets of closed empty pitfalls were inserted in non-trapping times to ensure pitfall traps were set in the same position for each of the four trapping events. The content of the pitfalls was washed by pouring it into a fine-meshed net and gently rinsing off the loose soil and propylene glycol with water. The remaining content was then preserved in 70 % alcohol.

The fauna were identified under a Leica-M Series Stereo-microscope and identified to order level. The ant specimens (Hymenoptera: Formicidae) were sorted to species, and named where possible. For each ant species collected, voucher specimens are held at the University of Stellenbosch. Sunspiders (Arachnida: Solifugae) and scorpions (Arachnida: Scorpiones) were sent to the American Museum of Natural History, for identification by L. Prendini.

Data Analyses

Weather data (rainfall and ambient temperature) were plotted for both the year in which sampling was conducted (2004) and the individual five-day sampling periods. Mean (± sd) values across the five day sampling period for maximum and minimum temperatures and wind, as well as median (± range) percentage relative humidity were compared across the seasons, using one-way ANOVA.

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Median (± range) percentage covers for each of the vegetation categories; bare, litter, grass, herbs and woody were used for each grid. The foliage height profile data was summarised as the total number of hits per four readings per pitfall, and then the mean number of hits per grid was determined (Bestelmeyer & Wiens 2001). Kruskal-Wallis tests were run for both cover and FHP's to determine significant differences between the seasons using the median and mean values per site.

Data from the pitfall traps were pooled into a single sample per grid. Although a variety of taxa were trapped in the pitfalls, only those taxa which could be classified as ground-dwelling were used (Uys & Urban 1998, Standen 2000). In the order Coleoptera, only individuals from the Tenebrionidae, Staphylinidae, Carabidae and Scarabidae families were considered. Arthropod data for each season, excluding ants, were grouped into functional groups, namely predators, herbivores, detiritivores, omnivores and others, which included arthropod taxa that could be assigned to more than one group (Scholtz & Holm 1996, Uys & Urban 1998, Picker *et al.* 2002). Beetles, which are functionally diverse, were separated into the previously mentioned families and then assigned to functional groups. Arthropod abundances were compared across the four seasonal sampling periods, by constructing rank abundance distributions for all arthropods across the four sampling periods (Magurran 2004). Additionally, rank abundance curves were constructed separately for ants and all other arthropods.

Only the ants were determined to species level and hence more in-depth analyses were able to be performed. To estimate sampling representivity of the ants, sample-based rarefaction curves were compiled separately for each of the four sampling events and also for the combined 2004 data set, using EstimateS V7, R.K. Colwell 2000, http://viceroy.eeb.uconn.edu/estimates. To compare species richness between seasons, sample-based rarefaction curves were rescaled to individuals, i.e. plotting observed species richness against individuals rather than samples (Gotelli & Colwell 2001). Species richness and abundance of ants were compared statistically across seasons using non-parametric Kruskal-Wallis tests and post-hoc Multiple Comparisons tests. To compare rank abundance distributions of various seasons, species rank abundance curves for ants were constructed. These curves were then further separated into reserve and remnant grids. Additionally, the numerically dominant ant species in each seasonal sample for each individual grid was tabulated. Simpson's (inverse) measure (calculated by Estimate S) was used to calculate an

evenness value ($E_{1/D} = \dfrac{1/D}{S}$, where D is the Simpson's Index and S the species richness) (Magurran 2004).

To determine whether species were characteristic of a season, Indicator values were determined using Dufrêne & Legendre (1997) Indicator Value Method. This method combines specificity (the uniqueness of a species in a season) with the fidelity (frequency in that season) and then provides an Indicator Value (IndVal) as a percentage for each species. High values indicate that the species is characteristic of the site, with species having significant values above 70 % regarded as a benchmark for indicator species (van Rensburg et al. 1999, McGeoch et al. 2002).

The ant genera were assigned to functional groups following Andersen (1995). Functional groups included, Sub-ordinate Camponotini (behaviourally submissive to more abundant, aggressive species), Hot Climate Specialists (adapted to arid environments), Cryptic Species (small body size, predominantly forage in soil and litter), Opportunists (unspecialized species, characteristic of disturbed sites, or other habitats supporting low ant diversity), Generalized Myrmicinae (ubiquitous, highly competitive taxa occurring in most habitats) and Specialist Predators (specialized diet, large body size and small colony size) (Hoffmann & Andersen 2003). Ant abundance was correlated with the abundance of other arthropod taxa, using Spearman's R, to determine whether ant abundance patterns mirrored those of other ground-dwelling arthropods.

To determine differences between ant assemblage structure of individual grids across seasonal samples, cluster analysis was used in Primer v5 (Clarke & Gorley 2001). Cluster analysis was based on group averaging and Bray Curtis similarity metric was used as a similarity measure (Clarke & Warwick 1994). Abundance data was standardized and fourth root transformed prior to analysis, so that common and rare species would be weighted equally (Clarke & Warwick 1994). To test for significant differences between seasonal samples, analysis of similarity (ANOSIM) was used. This non-parametric permutation procedure calculates a global R statistic from rank similarity matrices underlying sample ordinations. A significant global R close to 1 indicates distinct differences between assemblage structures of groups (Clarke & Warwick 1994). Non-metric multi-dimensional scaling (MDS) was used to display the relationship between assemblages of various seasons.

RESULTS

Weather data

During 2004, ambient temperature reached a maximum in autumn and a minimum in winter. Rainfall was highest during winter and only 0.1 mm fell in autumn (Fig. 1A). During the four five-day sampling periods, mean, maximum and minimum ambient temperatures were all significantly higher during autumn and summer than during winter and spring sampling periods (ANOVA, $F_{mean\ temp\ 1,3}$ = 23.03, $p < 0.001$; $F_{max\ temp\ 1,3}$ = 241.87, $p < 0.001$, $F_{min\ temp\ 1,3}$ = 30.45, $p < 0.001$). Seasonal temperature fluctuated within the five day sampling periods, with summer having the highest range (26.3 °C) and spring the smallest range (21.18 °C) (Fig. 1B).

Rainfall during the winter sampling period was 27 mm (over 3 days) and during the spring sampling period was 36 mm (over 3 days). Even though rainfall affects foraging activity of arthropods, rainfall was seen as part of the seasonal fluctuations and hence data of the winter and spring samples was still used. Mean wind speed and relative humidity did not differ significantly between seasons (ANOVA, $F_{1,3}$ = 0.50, $p > 0.05$ and ANOVA, $F_{1,3}$ = 2.19, $p > 0.05$ respectively) (Fig 2). Overall, a total of 370 mm rain fell during 2004, which is considerably less than the average annual rainfall of 500 mm (Midoko-Iponga 2004).

Vegetation

Percentage vegetation cover differed significantly over the seasons for litter (Kruskal-Wallis test; H = 38.28, df = 399, $p < 0.001$), for grass (Kruskal-Wallis test; H = 19.19, df = 399, $p < 0.001$), herbaceous component (Kruskal-Wallis test; H = 71.69, df = 399, $p < 0.001$) and the woody component (Kruskal-Wallis test; H = 24.67, df = 399, $p < 0.001$) (Fig.3). However overall percentage bare ground did not change significantly (Kruskal Wallis test: H = 1.77, df = 399, $p = 0.62$) (Fig. 3). There was significantly less litter in spring than all the other sampling periods and significantly more litter cover in winter than in summer. The percentage cover of the herbaceous component was significantly highest in spring compared to all other seasons and winter had a significantly lower herbaceous component than autumn and summer (Fig. 3).

Vegetation Height Profiles showed significant changes during the seasons in all lower height classes (up to 1.00 m) but not in the higher height classes (> 1.0 m) (Fig.

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4). Vegetation was most dense in the layer 0 - 0.25 m during spring. Summer vegetation had the highest density in the height classes 0.25 - 1.25 m and 1.50 m + of all the seasons and in the autumn sampling period density was highest for the height class 1.25 - 1.50 (Fig. 4). In general there was an increase in grass and litter in winter, while spring and summer had an increase in herbaceous and woody cover. Foliage density directly above the ground (0 - 0.25 m) was at its lowest in autumn and increased until spring after which it declined again.

Arthropods

A total of 28 839 ground-dwelling arthropod individuals were captured during the four sampling periods in Elandsberg. Sampling in summer yielded the highest number of individuals (14 251) and winter the lowest (1 566) (Table1). Overall, ants were the most abundant taxon trapped across all seasons (90 % in autumn, 84 % in winter and 91 % in spring and summer). Spiders (Arachnida: Araneae) were the second most abundant taxa captured in all samples except in spring, where beetles (Insecta: Coleoptera) were more abundant (Fig. 5 & 6). Peaks in arthropod abundances were different between orders across the seasons: scorpions (Scorpiones) and sunspiders (Solifugae) abundances peaked in autumn, earwigs (Dermaptera), millipedes (Diplopoda) and isopods in winter, termites (Isoptera), beetles (Coleoptera) and centipedes (Chilopoda) in spring, and finally bristletails (Archeognatha), silverfish (Thysanura), ants, pseudoscorpions and spiders in summer (Table1).

Sunspiders, scorpions and pseudoscorpiones were absent from the winter samples (Table1). Three scorpion species of the family Buthidae were found, namely *Parabuthus capensis* (Ehrenberg, 1831), *P. planicauda* (Pocock, 1889) and *Uroplectes variegates* (C.L. Koch, 1844). All scorpion species were present in the autumn samples, while *P. planicauda* and *Uroplectes variegates* were also present in spring and *Parabuthus capensis* was present in summer. All scorpion species were trapped in one reserve grid and only one species was trapped in a fragment grid. Five of the nine scorpions trapped were juveniles and two scorpions were female. Sunspiders could unfortunately not be identified to genus due to mostly juveniles being trapped and almost no adult males, which are necessary for identification (Prendini, personal communication). However it was possible to determine that some individuals were from the family *Ceromidae*. These sunspiders are very seldom

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collected and are distinguished from all other sunspiders by possessing tarsal claws on the reduced first pair of legs (Prendini, personal communication).

Excluding ants, more than half of the individuals captured across all seasons were predators, except for spring, where detiritivores had a slightly higher relative abundance (Fig. 7). Detiritivores were the second relatively most abundant group, peaking in summer and declining in winter. Herbivores were relatively more abundant during winter and spring than during the summer sampling periods. However, herbivore abundance was expected to be low in general, as herbivores are predominantly plant-dwelling and hence not likely to be caught in pitfall traps. Thus fluctuations in herbivore data could not be taken as reliable estimates of general fluctuations in herbivore abundance. Omnivore relative abundance was highest during winter (Fig. 7).

Ants

A total of 59 species were trapped at Elandsberg. Across combined seasonal and within seasonal samples, the ant species sampled were a representative sample of the fauna of Elandsberg, with rarefaction curves approaching asymptotes (Fig. 8A & B) (see also Chapter 1). Both ant abundance and species richness were highest in summer and lowest in winter, with significantly higher species richness in autumn and summer compared to winter (Kruskal Wallis test, H = 18.37, d.f. = 3, p < 0.001) (Table 2). Species density (i.e. number of species per sample) increased similarly for reserve and remnant sites during the summer months, while during winter and spring, species density of remnant sites was higher than reserve sites (Fig. 8A). Remnant sites showed a steeper accumulation of species richness (i.e. number of species per individual) compared to reserve sites, for spring and summer and for overall species richness (Fig. 8B). The rank abundance curves for ants changed across the seasons with relative dominance being low during autumn and winter sampling periods, compared to the spring and summer sampling periods (Fig. 9). This was confirmed by the Simpson's evenness values; autumn (0.189) and winter (0.107) had values closer to one than spring (0.060) and summer (0.057).

Anoplolepis steingroeveri was numerically dominant in spring and summer, while in autumn and winter it was the second most abundant ant (Fig. 9, Appendix A). *Pheidole* sp.1 was numerically dominant in winter, but also retained a relatively high abundance across the other seasons (Fig. 9, Appendix A). Dominance of individual

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species per grid changed across seasons, with the exception of three grids, two of which were dominated by *Anoplolepis steingroeveri* and one dominated by *Pheidole* sp.1 (Table 3). The spring samples had six species that were not trapped in any of the other seasons, whereas in winter there was only one such species (Table 2). One species was a characteristic indicator of spring samples (*Messor* sp. 2, IndVal = 70.36, $p < 0.05$) and one of autumn samples (*Ocymyrmex* sp. 1, IndVal = 72.07, $p < 0.05$). No species were characteristic of winter or summer samples. When including significant Indicator Values above 50 (i.e. lowering the subjective benchmark), two species were characteristic of summer samples (*Camponotus vestitus,* IndVal = 54.09, $p < 0.05$ and *Ocymyrmex* sp. 2, IndVal = 63.46, $p < 0.05$) and two additional species of autumn samples (*Lepisiota* sp.2, IndVal = 50.89, $p < 0.05$ and *Monomorium* sp.1, IndVal = 58.31, $p < 0.05$).

Assemblage structure differed significantly, but only by a small amount, between seasons (Global R = 0.18, $p < 0.001$, Fig. 10). Autumn assemblage structure was significantly different to that of winter (R = 0.30, $p < 0.01$) and spring (R = 0.25, $p < 0.001$), but not summer (R = 0.02, $p > 0.05$). Summer assemblage structure was also significantly different to winter (R = 0.28, $p < 0.01$) and spring R = (0.24, $p < 0.01$). Winter assemblage structure did not differ significantly from spring samples (R = -0.025, $p > 0.05$). Assemblage structure was also significantly different between pooled autumn and summer samples and pooled spring and winter samples (Global R = 0.28, $p < 0.01$). Large differences, i.e. high R-values, between ant assemblage structures of seasonal samples were not observed, but they were nonetheless significant.

The composition of functional groups changed across seasons (Fig. 11A & B). Generalised Myrmicinae had the highest relative abundance during autumn and spring, while Hot Climate Specialists were proportionally most abundant in spring and summer (Fig 11A). Proportional abundances of Cryptic species, Subordinate Camponotini and Specialist Predators remained rare throughout the four seasonal samples. Opportunist species had their highest proportional abundance in autumn. Proportional species richness showed a different pattern, with Opportunist Species having the highest proportion of species across all seasons (Fig. 11B). Cryptic Species were absent from autumn and winter samples (Fig. 11B).

Ant abundance data per pitfall (n = 400) across the four seasonal samples were significantly positively related to several taxa, namely silverfish ($r_s = 0.40$, $p < 0.05$),

bristletails (r_s = 0.16, p < 0.05), beetles (r_s = 0.20, p < 0.05), pseudoscorpions (r_s = 0.20, p < 0.05) and spiders (r_s = 0.36, p < 0.05). Isopods (r_s = -0.15, p < 0.05), sunspiders (r_s =-0.20, p < 0.05) and millipede (r_s = -0.15, p < 0.05) abundances were significantly negatively correlated with ant abundance. Termites, cockroaches, earwigs, scorpions and centipedes were not significantly correlated with ant abundance (p > 0.05).

DISCUSSION

Arthropods

Substantial seasonal variation in abundance and composition was observed in the ground-dwelling arthropod community of this area of the CFR. Arthropod abundance generally exhibited a peak in summer and a trough in the winter; a pattern that is well known for arthropods in Mediterranean habitats and has been previously quantified for epigaeic fauna (Andersen 1986, Magagula 2003, Stamou *et al.* 2004). Abundance peaks in summer and troughs in winter are generally related to temperature fluctuations, as arthropod growth rates and adult reproductive activity are determined and influenced by temperature (Wolda 1988, Speight *et al.* 1999).

However, seasonality patterns tend to be much more complex than simply related to temperature and reflect responses to not only weather conditions but also biotic conditions such as predator/parastitoid presence and food resources (Wolda 1988). Peaks in abundances, as exhibited by termites, beetles and centipedes in this study, are most likely responses to a combination of rainfall and temperature and resulting increased food resources (Newell 1997, Bolger *et al.* 2000) (Fig 1A).Vegetation (including litter) density, complexity and diversity have also been shown to affect arthropod assemblages (Visser *et al.* 1999, Bolger *et al.* 2000, Retana & Cerdá 2000, Harris *et al.* 2003, Magagula 2003), although effects vary between taxa. Increased cover and density of the herbaceous component and woody species during spring may provide an increase in food resources for herbivorous species, such as certain beetles and termites. This was found in a previous study in the CFR, where insect biomass, mainly including herbivorous taxa, showed spring peaks (Schlettwein & Giliomee 1987).

Winter peaks in abundances were seen for earwigs, millipedes and isopods in this study. Millipedes are dependent on moisture and many species avoid direct sunlight

and dry heat (Druce *et al.* 2004), hence cooler, wetter winter months are likely to be most favourable for this taxon. The response of individual orders to seasonal changes is complicated, because individual species within orders frequently have different responses depending on their life history characteristics to biotic and abiotic variables (Wolda 1988, Pinheiro *et al.* 2002). Also abundance fluctuation within seasons and across years may vary, a trend which was not investigated in this study (Wolda 1988, Tylianakis *et al.* 2005).

Functional group composition, excluding ants, showed clear seasonal variation. Predators were the dominant group throughout the four seasons, while relative abundances of detiritivores and omnivores varied considerably across seasons. The abundance of detritivores, which are reliant on food resources found in the litter layer, showed no obvious relationship with the percentage litter cover at each sampling grid; the percentage litter layer was highest during winter, however the relative abundance of detritivores was lowest. It may however be that litter depth is a better correlate to detritivore abundance than percentage litter cover. Alternatively a more accurate collection method for detritivores would have been litter sampling. Nonetheless, some of the detritivore taxa, namely millipede and isopod abundances did peak in winter with a peak in the litter component.

The high relative abundance of predators is a consequence of high spider abundance with spiders being the second most abundant order found in Elandsberg. Spiders and predatory beetles, such as Carabids, are known to be abundant and dominate ground dwelling arthropods in regions of Europe, USA and Australia (Bolger *et al.* 2000, Woinarski *et al.* 2002). They are commonly found in agricultural lands, playing an important role in controlling pest species, and are known to be active all year round (Booij & Noorlander 1992, Dippenaar-Schoeman & Jocqué 1997). The high number of predators in Elandsberg is a positive sign for the pest management of agricultural landscapes. Other predators such as sunspiders, pseudoscorpions and scorpions appear to be dependent on higher temperatures for activity (Leeming 2003), explaining why none were found during winter sampling.

Ants

The Formicidae dominated the epigaeic fauna across all seasons. A total of 59 species were captured in Elandsberg, which is higher than that reported for other areas of the CFR (see Chapter 1); many of these studies however only conducted sampling

in one season. Two studies, which investigate ant assemblages across more than one season, were conducted in Jonkershoek, Cape Floristic Region and captured only 45 and 31 species (Donnelly & Giliomee 1985, Schlettwein & Giliomee 1987), however Dietrick Vacuum Sampling was used in the second study which may have underrepresented ant species richness of the area. In the semi-arid Karoo, samples were taken in summer and winter resulting in 45 species caught in pitfall traps (Lindsey & Skinner 2001). A study in the Cederberg, CFR, sampled ants in autumn and spring and captured 45 species in the Proteoid fynbos (Botes *et al.* 2006). Species richness of the ants from the CFR is estimated to be 100 species, although this is most likely an underestimate (Giliomee 2003). Nonetheless it indicates that Elandsberg ant richness is comparatively high.

The patterns of seasonal variation in ants resembled that of epigaeic arthropods in general, with ant abundance and species richness peaking in summer and declining in winter. This pattern has been found in several other studies (Andersen 1986, Lobry DeBruyn 1993, Newell 1997, Lindsey & Skinner 2001). Ants are a thermophilic taxa with activity strongly linked to temperature (see Andersen 1997, Kaspari 2000). In addition, temperature in Mediterranean areas has been shown to control the structure and composition of epigaeic ant assemblages (Cerdá *et al.* 1998, Retana & Cerdá 2000). Hence increased ant abundance and richness in the summer can be attributed in part to higher temperatures which favour increased foraging and activity. Ant assemblage composition structure showed similar results, with the warmer months (summer and autumn) having similar composition structures, but differing from those of cooler months (spring and winter).

Individual species however differed in their response to temperature fluctuations. Some appeared to be directly related to temperature, such as the strongly thermophilic genera, *Ocymyrmex* (Marsh 1988). For these species optimal ground surface temperatures for foraging activity are above 50 °C (Witt & Giliomee 1999). *Ocymyrmex* sp.1 dominated numerically during autumn in general and *Ocymyrmex* spp 1 & 2 were the numerically dominant species in six of the ten grids in autumn or summer or in both seasons. *Ocymyrmex* sp.1 was a characteristic indicator species for autumn samples, while *Ocymyrmex* sp. 2 was characteristic for summer samples. Hence the species abundance patterns reflected that of temperature increases.

For other species, seasonal fluctuations in abundance appeared to be controlled both by weather conditions and food availability. This is characteristic for ant

assemblages in strongly seasonal climates (Andersen 1986). Food availability is likely to have increased during spring and summer, as vegetation cover of particularity the herbaceous and woody component increased. Hence ant richness and abundance were expected to peak in spring, a pattern shown in several other studies, some of which were conducted in Mediterranean regions (Schlettwein & Giliomee 1987, Samways 1990, Kaspari 2000). However overall spring peaks for ant abundance and species richness were not seen in this study. Temperatures for spring in this study may have been lower than that of other studies and rainfall may have been responsible for reduced forager activity (Andersen 1997, Bestelmeyer *et al.* 2000, Kaspari 2000).

Nonetheless certain species did show abundance peaks during spring, such as *Messor* species, which are known seed-harvesters (Hölldobler & Wilson 1990). These species were numerically dominant during spring in two grids, and *Messor* sp. 2 was shown to be characteristic of spring samples. This was probably due to the availability of seeds during spring (Johnson 1992). Cryptic Species, including *Solenopsis* and *Plagiolepis* species, were found only during spring and summer, possibly also responding to increased temperatures and food availability. However these species are mostly soil and litter foragers (Hoffmann & Andersen 2003) and hence would not have been adequately trapped by pitfall traps. Thus no clear conclusion can be drawn from these.

Another example of an ant species controlled by both weather and climate variability, was *Anoplolepis steingroeveri*, the most dominant ant species trapped in this study. This pugnacious species is widespread throughout southern Africa and known to dominate pitfall traps where it occurs (Addison & Samways 2000). *Anoplolepis* species are able to forage over a wide range of soil temperature, from 10 – 54 °C, although they appear to prefer soil temperatures between 20 - 24°C (Witt & Giliomee 1999). In this study, *A. steingroeveri* was overwhelmingly numerically dominant in spring and summer samples and was also dominant in two grids throughout the year. This species was also the main contributor to the high relative abundance of Hot Climate Specialists during summer and spring. High abundances of *A. steingroeveri* in spring and summer thus appear to response to an increase in temperature as well as food availability.

Studies have shown temperature to be more important in structuring ant assemblages than interspecific competition, especially if thermal variations are high (Cerdá *et al.* 1998, Retana & Cerdá 2000). Species vary in their thermal tolerances so

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that different species are active during different times of the day and year, which reduces competition and allows species to co-exist. In the assemblage studied here, the reduction of *A. steingroeveri* abundance during autumn may be explained by this species thermal tolerance levels. Autumn samples were taken during the warmest month (February) and ground temperatures are likely to have been highest during this sampling period. Although summer ambient temperatures were higher than in autumn during the five-day trapping period, shading (represented by an increase in woody component and vegetation density above 1.5 m) was greater in summer than autumn and hence reduced soil temperatures, which affects ants more directly (Retana & Cerdá 2000, Lassau & Hochuli 2004). Therefore too high temperatures may have been the cause of reduced *A. steingroeveri* abundance during autumn. Declines in this dominant species, resulted in greater assemblage evenness during this month (evenness was highest in autumn), allowing the relative abundance of other species to increase. Some of the species that increased in abundance during autumn were Opportunist Species, including *Tapinoma, Technomyrmex, Lepisiota, Cardiocondyla* and *Tetramorium.* These species are generally unspecialized and poor competitors. Their distribution is known to be highly influenced by the presence of other ants, and they predominate only where conditions for other ants are unfavourable (Andersen 2000). Hence high temperatures during autumn allowed Opportunist Species to increase in relation to dominant species such as *A. steingroeveri.*

Thermal tolerance levels may also have limited the abundance of *Pheidole* sp.1 which in this study was numerically dominant in winter. *Pheidole* species appear to be intolerant of surface temperatures above 35 °C (Witt & Giliomee 1999) and would thus be mostly active during the cooler seasons of the year. Since this species was one of the main contributors to the Generalized Myrmicinae, this would also explain the relative increase in GM abundance during winter. For most other species, decreased temperatures in winter, led to reduced ant abundance and foraging activity.

Therefore in general, summer peaks in ant abundance and species richness may be seen as a general optimal combination of ground surface temperature and food availability. Spring was still relatively cool, while autumn was possibly too warm for several species.

Ant abundance cycles across the seasons were most closely followed by that of silverfish and spiders. Since many ant species are also predators it is not surprising to find seasonal cycles in abundance of spiders and ants to be similar. Although we were

unable to compare whether species richness of ants mirrored that of the remaining ground-dwelling arthropods species (due to arthropods not being identified to species level) studies conducted in Australia, showed species richness of ants to be significantly positively correlated to that of collembola, beetles and termites (Alonso 2000). However this result is dependent on the habitat in which sampling is conducted, since other studies found beetles species richness to have no correlation with ant species richness and termites to be negatively correlated to ant species richness (Alonso 2000).

In conclusion, seasonal variation in epigaeic arthropods in Elandsberg is characterized by a general abundance peak in summer and trough in winter. Abundance peaks for individual taxa however differed across the year. Ants dominated the arthropod fauna, while spiders and beetles were also abundant, emphasizing the importance of ants in the CFR lowlands. Ant species richness as well as abundance fluctuations mirrored that of the general arthropod pattern and reflected a response to fluctuations in temperature and food availability. Thus results for ants have a broader relevance for ground dwelling arthropods in the region.

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Table 1 Mean ± standard deviation and occupancy (percentage of grids at Elandsberg occupied) of ground-dwelling arthropod abundances captured using pitfall trapping at Elandsberg, Western Cape during 2004 in four seasonal samples. Functional Groups (FG) are as follows D = detiritivore, O = omnivore, H = herbivore and P = predator.

Taxa	Autumn		Winter		Spring		Summer		Total		FG
	Mean ± sd	Occ	Mean ± sd	Occ	Mean ± sd	Occ	Mean ± sd	Occ	Mean ± sd	Occ	
CLASS INSECTA											
Order Archaeognatha	0	0	0	0	5.8 ± 7.1	70	7.0 ± 8.9	80	3.2 ± 6.4	37.5	D
Order Thysanura	14.8 ± 5.2	100	0.1 ± 0.3	10	2.80 ± 1.9	80	27.5 ± 15.1	100	11.3 ± 13.4	72.5	D
Order Blattodea	0.4 ± 1.0	20	0.2 ± 0.6	10	0	0	0.5 ± 0.7	40	0.3 ± 0.7	17.5	O
Order Isoptera	0.8 ± 2.2	20	1.9 ± 2.7	40	3.8 ± 7.4	50	0.4 ± 0.5	40	1.7 ± 4.2	37.5	H
Order Dermaptera	0	0	1.6 ± 1.3	80	0.5 ± 0.7	40	0.1 ± 0.3	10	0.6 ± 1.0	32.5	O
Order Coleoptera	8.3 ± 6.8	100	6.8 ± 5.3	90	32.9 ± 29.4	100	27.4 ± 34.5	100	18.9 ± 25.0	97.5	P & D
Order Hymenoptera (Formicidae)	506.5 ± 158.8	100	131.9 ± 102.0	100	669.2 ± 1216.9	100	1298.5 ± 2455.2	100	651.5 ± 1386.8	100	-
OTHER HIGHER TAXA											
CLASS ARACHNIDA											
Order Solifugae	4.3 ± 3.4	90	0	0	0.1 ± 0.3	10	1.4 ± 1.1	80	1.5 ± 2.5	45	P
Order Scorpiones	0.5 ± 0.7	40	0	0	0.2 ± 0.6	10	0.1 ± 0.3	10	0.2 ± 0.5	15	P
Order Pseudoscorpiones	4.8 ± 5.2	90	0	0	0.8 ± 1.1	40	5.2 ± 5.4	80	2.7 ± 4.3	52.5	P
Order Araneae	24.9 ± 12.7	100	9.8 ± 4.1	100	16.10 ± 7.6	100	56.60 ± 40.8	100	26.8 ± 27.8	100	P
CLASS DIPLOPODA	0.1 ± 0.3	100	3.1 ± 5.1	40	1.30 ± 2.7	30	0.3 ± 0.3	20	1.2 ± 3.1	25	D
CLASS CHILOPODA	0.1 ± 0.3	100	0.3 ± 0.7	20	3.10 ± 4.2	70	0.1 ± 0.7	10	0.9 ± 2.4	27.5	P
CLASS MALOCOSTRACA											
Order Isopoda	0	0	0.9 ± 1.1	50	0.1 ± 0.3	10	0	0	0.3 ± 0.7	15	D
TOTAL	59.0 ± 17.6	100	24.7 ± 9.6	100	67.5 ± 35.1	100	126.6 ± 56.6	100	69.5 ± 50.0	100	

Table 2 Species richness and abundance of ants captured in Elandsberg across four seasons. Means with no letters in common are statistically different (p < 0.05).

Season	Observed species richness	Mean ± standard deviation (n = 10)	Predicted species richness (Chao 2)	Number of individuals	Number of unique species
Summer	46	18.4 ± 4.62 **a**	46.63 ± 1.36	12985	5
Autumn	43	16.4 ± 2.63 **a**	43.57 ± 0.85	5065	2
Spring	42	13.2 ± 5.25 **ab**	43.02 ± 0.98	6692	6
Winter	32	8.7 ± 3.23 **b**	32.61 ± 0.99	1319	1
All	59		59.16 ± 0.15	26061	

Table 3 Sampling grid description and dominant Formicinae species (relative abundance (percentage) per grid) present at each of the four seasonal sampling periods. A. ste = *Anoplolepis steingroevri*, Ocy = *Ocymyrmex*, Phe = *Pheidole*, Mes = Messor, Tet = *Tetramorium*

Grid	Description of grid	Dominant ant species			
		Autumn	Winter	Spring	Summer
Reserve					
A	BIOTA observatory Swartland Alluviam Fynbos	*A. ste* (39.7%)	*A.ste* (59.1%)	*A.ste* (50.5%)	*A. ste* (59.8%)
B	Swartland Alluviam Fynbos	*Ocy* sp.1 (39.6%)	*Phe* sp.1 (69.5%)	*Phe* sp.1 (44.6%)	*Tet* sp.2 (24.9%)
C	Swartland Shale Resnosterveld	*A.ste* (83.2%)	*A.stei* (99.4%)	*A.stei* (99.9%)	*A.stei* (99.2%)
D	Swartland Alluvium Fynbos	*Ocy* sp.1 (40.7%)	*Phe* sp.1 (51.7%)	*Phe* sp.1 (49.4%)	*Ocy* sp.2 (44.9%)
E	Swartland Alluvium Fynbos	*Ocy* sp.1 (27.1%)	*Phei* sp.1 (60.8%)	*Phe* sp.1 (57.0%)	*Ocy* sp.2 (37.3%)
Remnant					
F	Fragment on rocky ridge surrounded by wheat fields	*Phe* sp.1 (41.8%)	*Phe* sp.1 (76.0%)	*Phei* sp.1 (50.6%)	*Phe* sp.1 (24.9%)
G	Old field with recovering vegetation	*Ocy sp.*1 (25.4%)	*Phe* sp.1 (81.5%)	*Phei* sp.1 (40.1%)	*Tet* sp.2 (22.5%)
H	Old field with recovering vegetation	*Tet* sp.2 (22.2%)	*Phe* sp.1 (30.0%)	*Mes* sp.2 (47.5%)	*Phe* sp.1 (18.2%)
I	Vlei area surrounded by wheat fields	*Ocy* sp.2 (31.5%)	*Phe* sp.1 (24.0%)	*Mes* sp.2 (61.5%)	*Ocy* sp.1 (41.0%)
J	Fragment surrounded by wheat fields	*Ocy* sp.1 (31.3%)	*Ph* sp.1 (53.8%)	*Phei* sp.1 (47.6%)	*Ocy* sp.2 (30.0%)

A
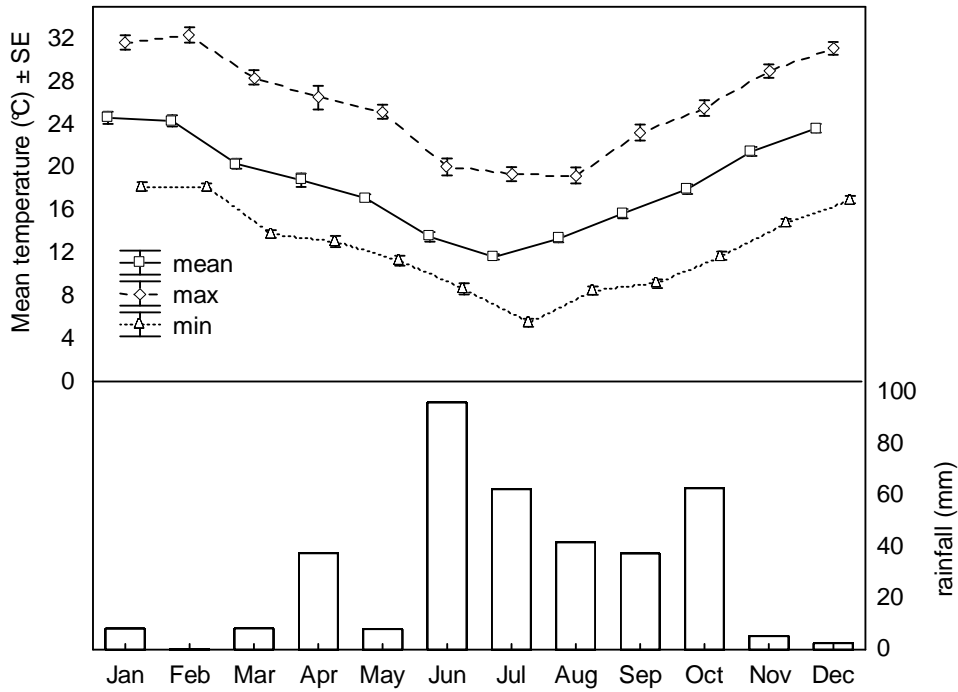
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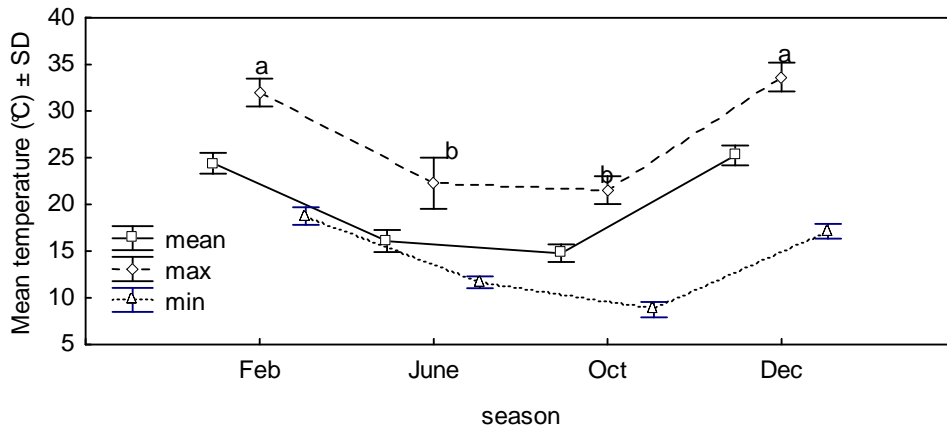
Figure 1A Total rainfall and ambient temperatures (mean, maximum and minimum) in 2004 and **B** temperatures (mean, max and min) over four, five-day sampling periods in Elandsberg. Means bearing the same letter indicate values that are not significantly different at the 5% level. Data from Diemerskraal Weather Station (33.35°S, 18.55°E), provided by AgroMet-ISCW Agricultural Research Council.

A
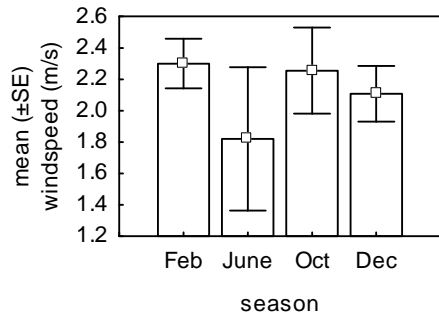
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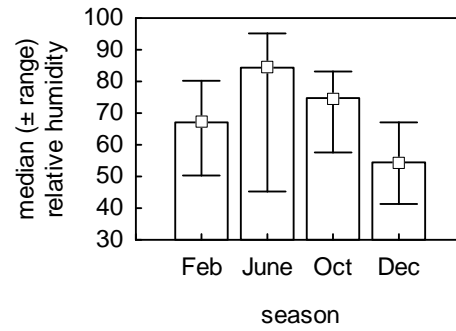
Figure 2A Mean wind speed and **B** median relative humidity of five day sampling periods across seasonal samples at Elandsberg 2004. Data from Diemerskraal Weather Station (33.35°S, 18.55°E), provided by AgroMet-ISCW Agricultural Research Council.
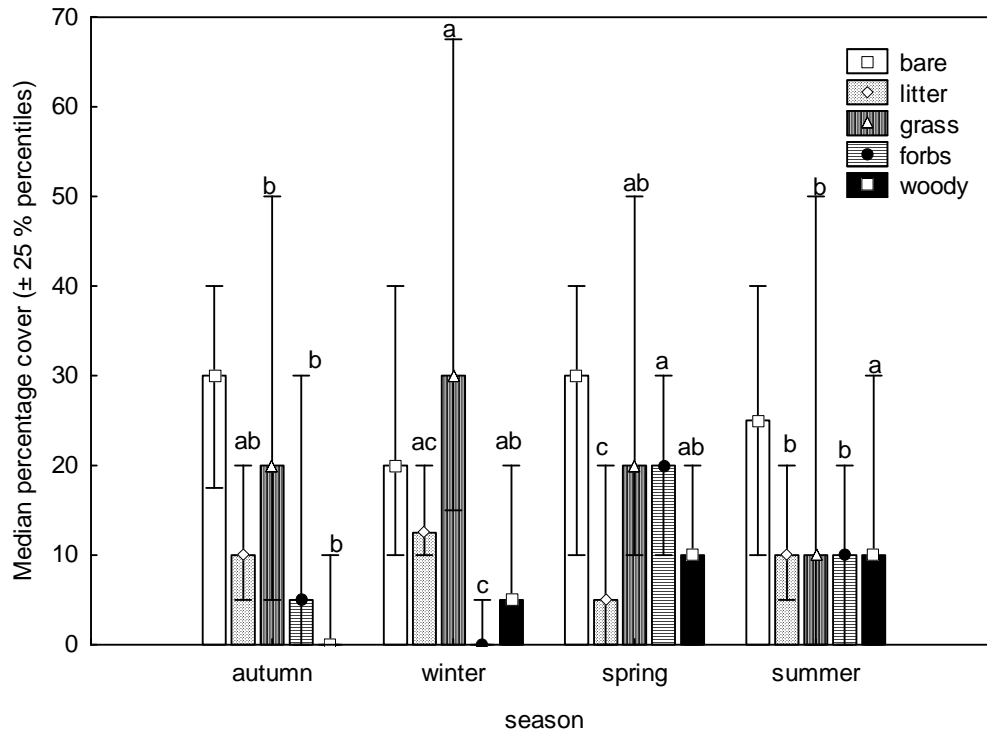
Figure 3 Median percentage vegetation covers for bare, litter, grass, herbaceous component and woody, across four seasons. The bars bearing the same letter indicate medians that are not significantly different at the 5 % level.
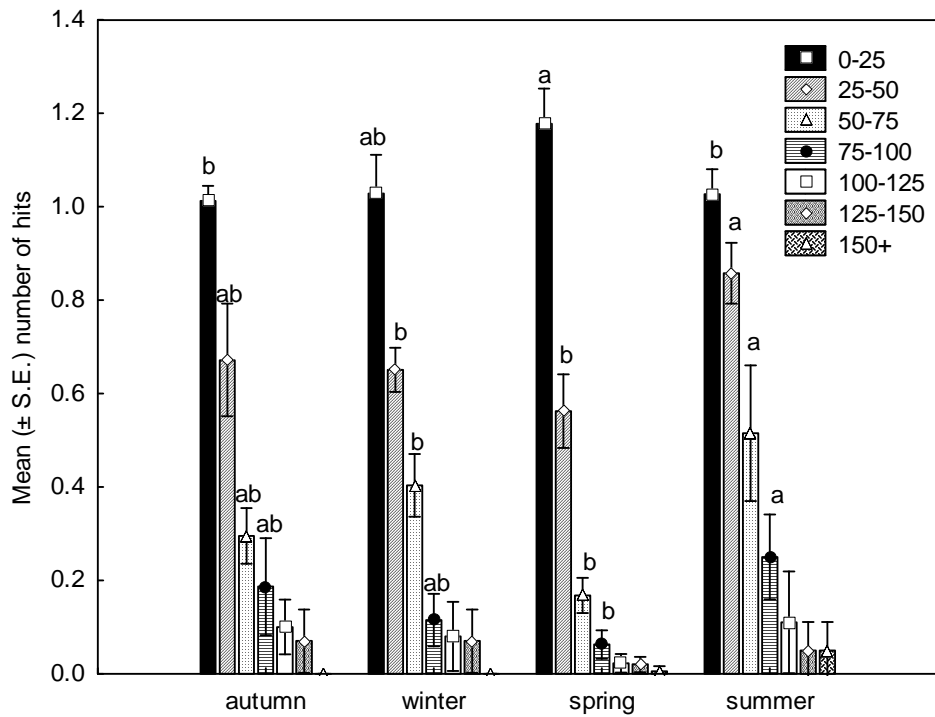
Figure 4 Mean number of hits for each of seven height classes (in cm) across the four seasons at Elandsberg (n = 10). The bars for each height class bearing the same letter indicate means that are not significantly different at the 5 % level.
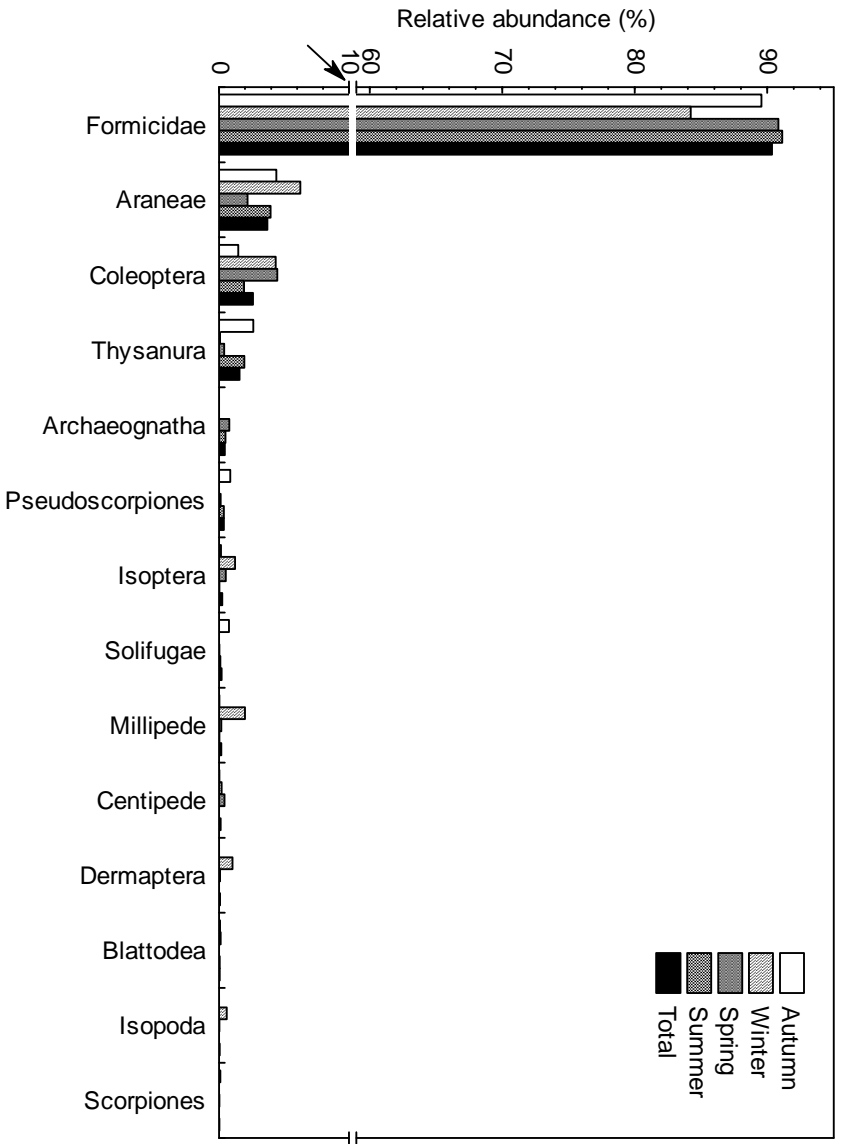
Figure 5 Arthropod relative abundance distributions of four seasons, at Elandsberg.

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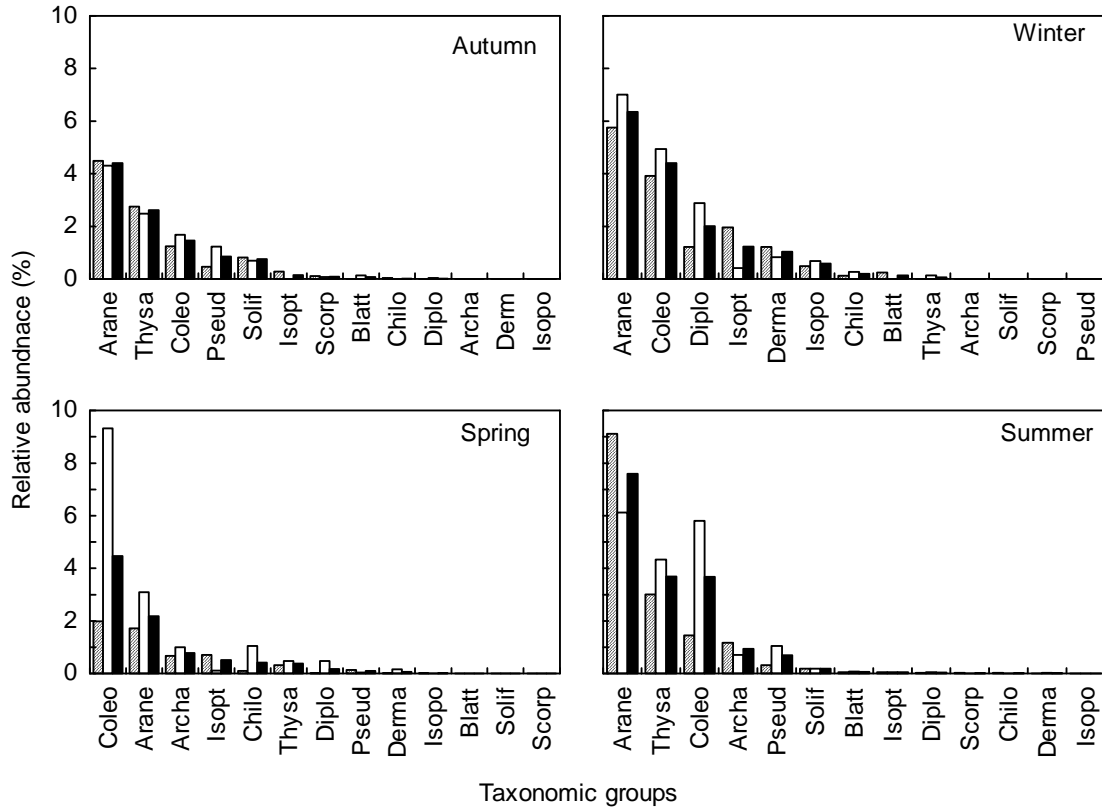
Figure 6 Relative arthropod abundance distribution, **excluding ants**. Diagonally striped bars = reserve grids, horizontally striped bars = remnant grids and solid bars = complete data sets. Arane = Araneae, Archa = Archaeognatha, Blatt = Blattodea, Chilo = Chilopoda, Coleo = Coleoptera, Derma = Dermaptera, Diplo = Diplopoda, Isopo = Isopoda, Isopt = Isoptera, Pseud = Pseudoscorpiones, Scorp = Scorpiones, Solif = Solifugae, Thysa = Thysanura.

Autumn

Winter

Spring

Summer

Detritivores;	Herbivores	Omnivores	Predators	Others
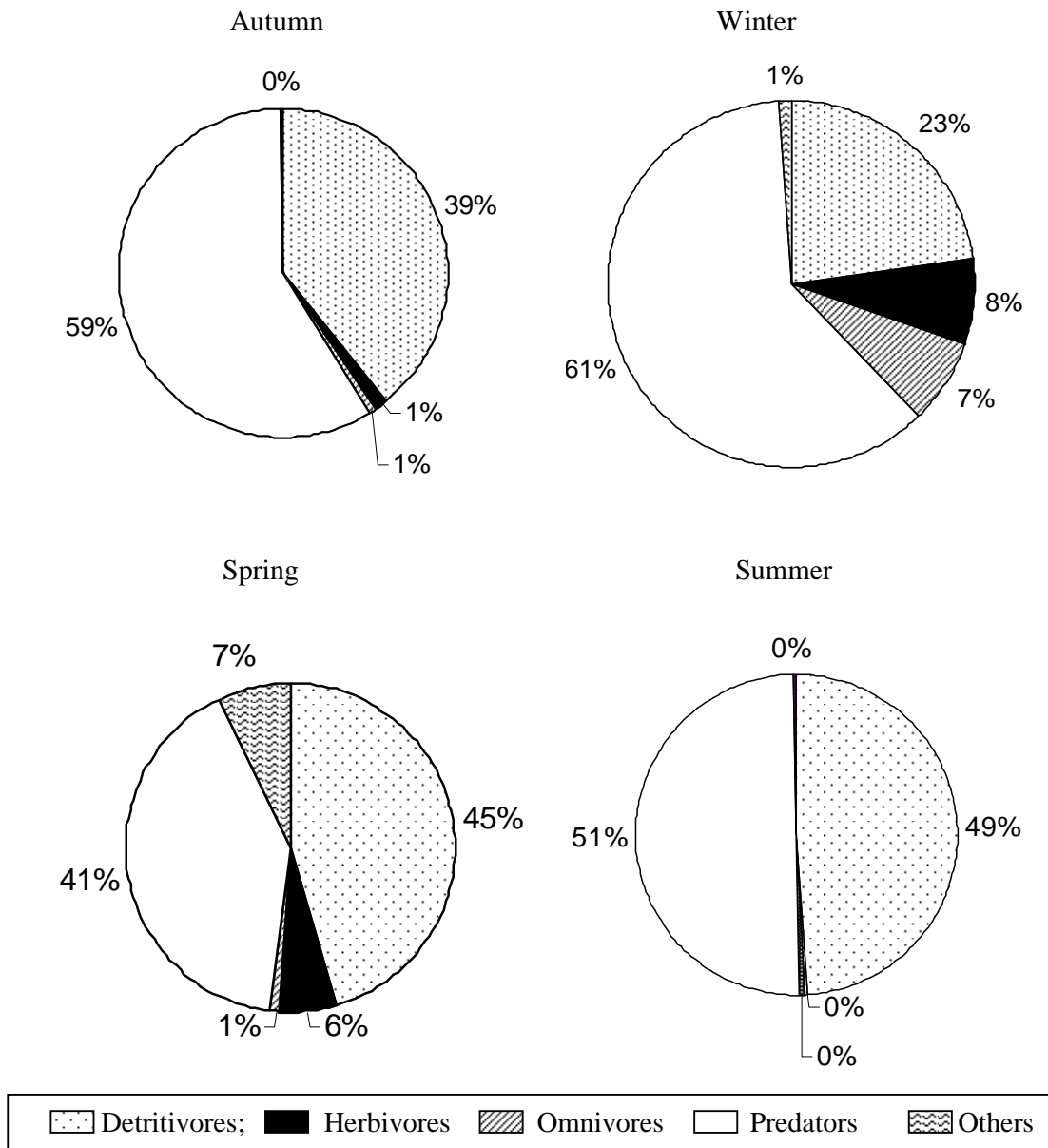
Figure 7 Relative abundances of arthropod functional groups (excluding ants) across the four seasons.

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A

B
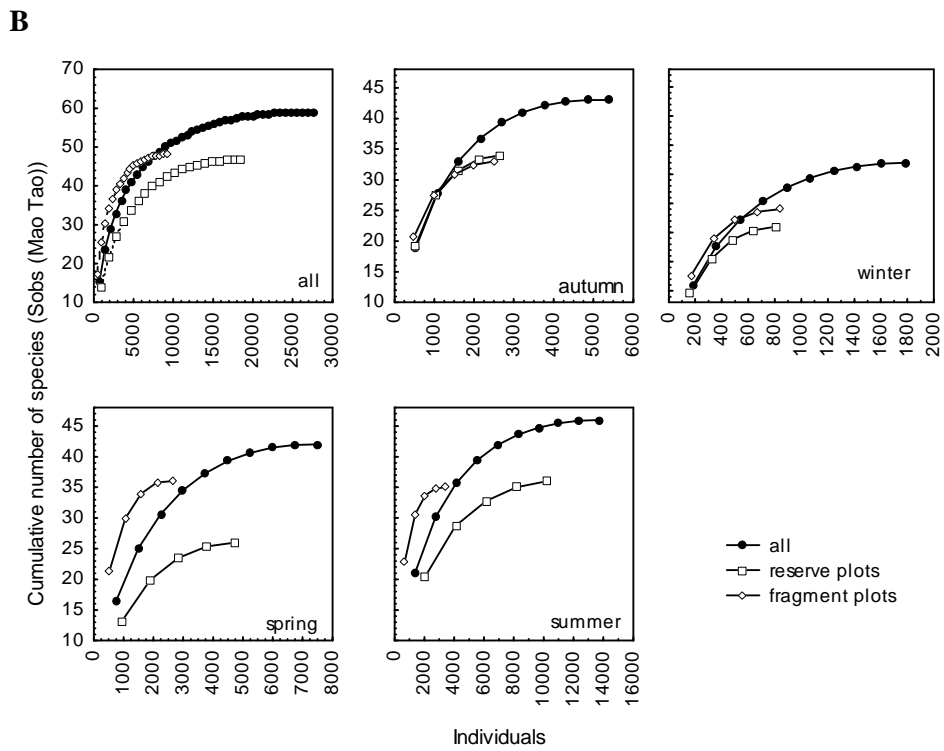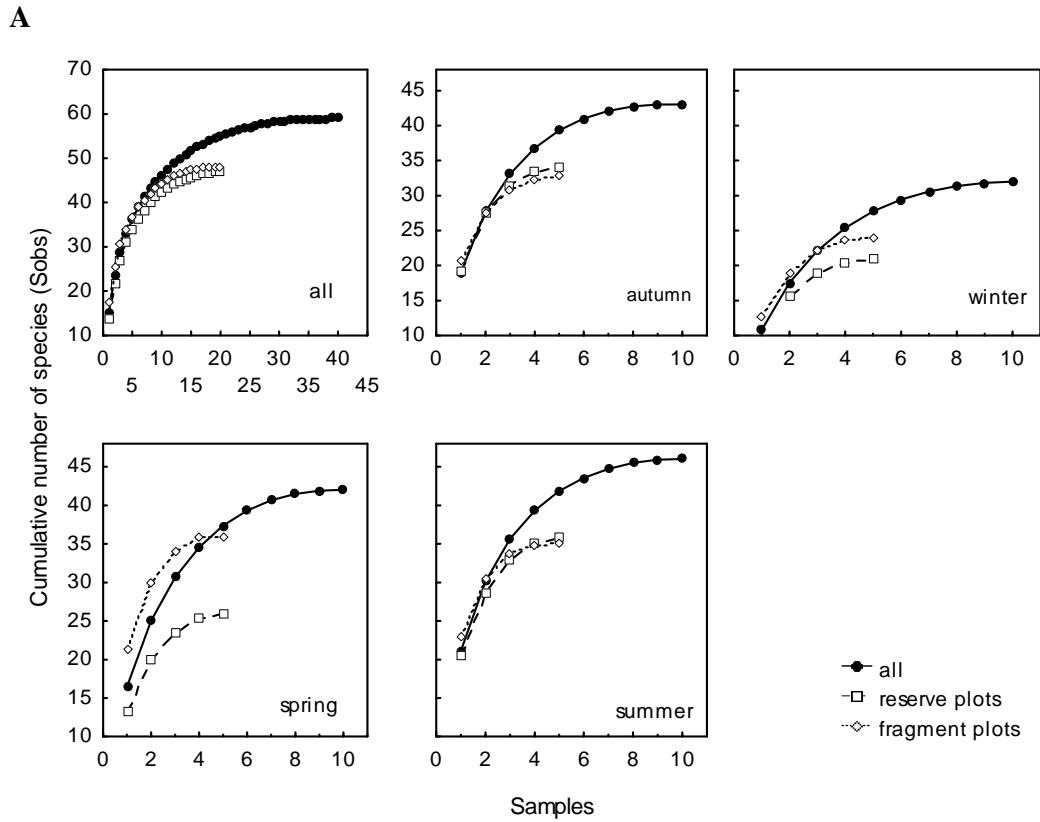
Figure 8 Sample-based rarefaction curves of **A** species richness and samples and **B** species richness and individuals for ants caught across four seasons at Elandsberg.

66
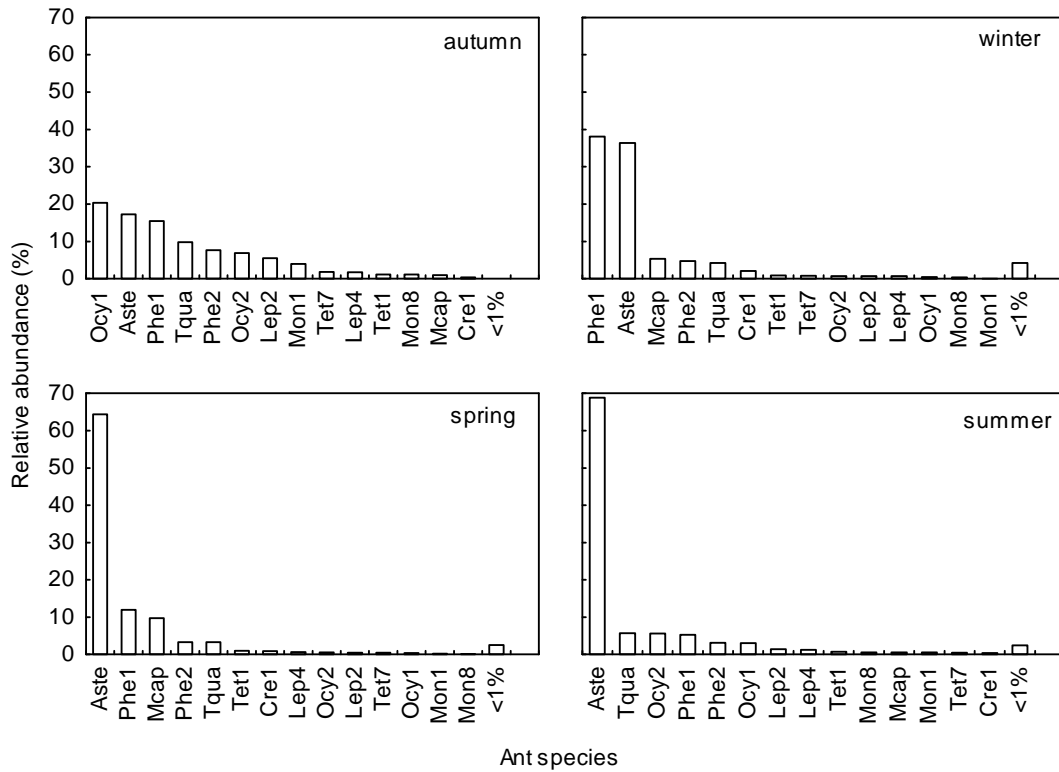
Figure 9 Ant relative abundance distributions across four seasons in Elandsberg. Species with a relative abundance of less than one percent were added together in the last column (< 1 %). See Appendix A for species abbreviations.
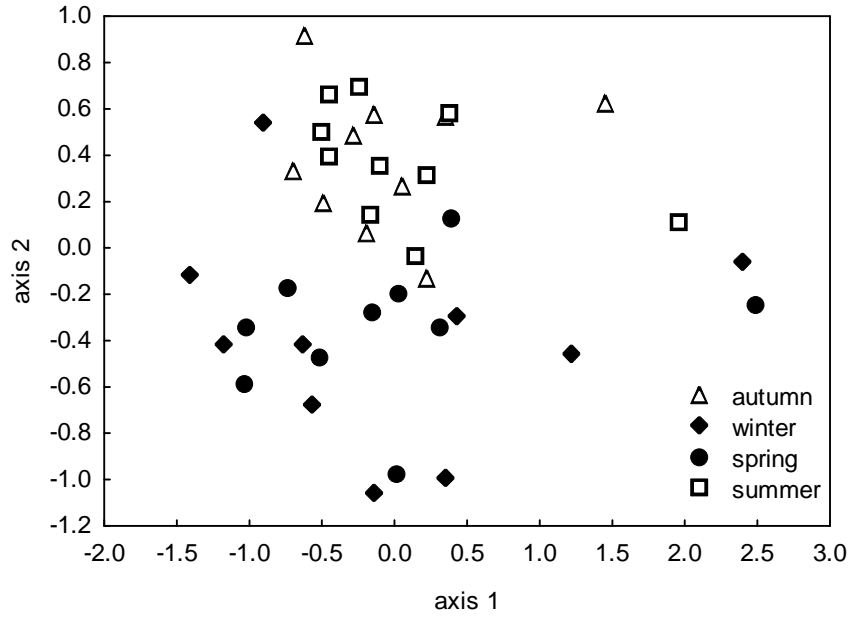
Figure 10 Non-metric multi-dimensional scaling (MDS) ordination of ant assemblage structure at Elandsberg across four seasons. Grids from the same seasonal sample are given the same symbol (Global R = 0.175; p < 0.01; stress = 0.17).

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A

B
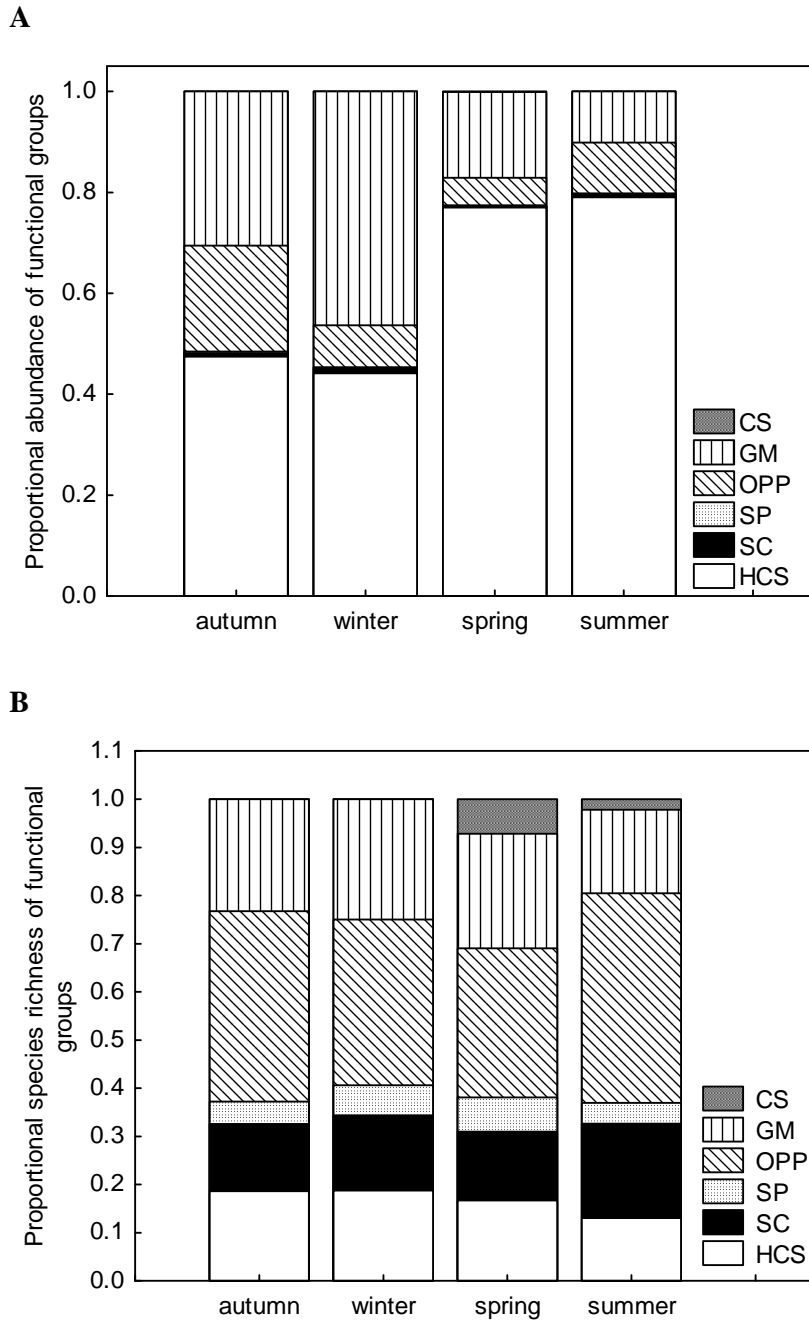
Figure 11A Relative abundance and **B** species richness of ant functional groups at Elandsberg, across four seasons. CS = Cryptic species, GM = Generalized Myrmicinae, OPP = Opportunists, SP = Specialist Predators, SC = Subordinate Camponotini and HCS = Hot Climate Specialists.

APPENDIX

Appendix A: Ant species and their abundances at Elandsberg across four seasons.

Species	abbrev	Autumn	Winter	Spring	Summer	Total
Cerapachynae						
Cerapachys sp.1	Cer1	0	0	2	0	2
Dolichoderinae						
Tapinoma sp.1	Tap1	0	0	0	12	12
Technomyrmex albipes (F. Smith)	Talb	0	0	8	1	9
Technomyrmex sp.1	Tec1	5	0	0	1	6
Formicinae						
Anoplolepis custodiens (F.Smith)	Aste	874	480	4310	8942	14606
Anoplolepis sp.1	Ano1	18	0	1	0	19
Anoplolepis sp.2	Ano2	4	0	0	0	4
Camponotus sp.1 (*emarginatus* gp)	Cam1	6	6	6	7	25
Camponotus sp.2	Cam2	4	2	6	10	22
Camponotus vestitus (F. Smith)	Cam3	15	0	2	55	72
Camponotus mystaceus (Emery)	Cam4	0	4	3	4	11
Camponotus sp.5	Cam5	2	0	0	1	3
*Camponotus maculatus-*group	Cam6	1	1	0	3	5
Camponotus angusticeps (Emery)	Cam9	0	0	0	6	6
Camponotus sp.12	Cam12	0	0	1	0	1
Camponotus sp.13	Cam13	0	0	1	2	3
Camponotus fulvopilosus (DeGeer)	Cful	7	1	0	2	10
Lepisiota sp.1	Lep1	4	0	5	8	17
Lepisiota sp.2	Lep2	279	10	31	187	507
Lepisiota sp.3	Lep3	8	2	4	28	42
Lepisiota sp.4	Lep4	87	10	42	159	298
Lepisiota sp.5	Lep5	13	0	4	25	42
Lepisiota sp.6	Lep6	1	0	0	2	3
Lepisiota sp.7	Lep8	3	0	0	1	4
Plagiolepis sp.1	Pla1	0	0	2	0	2
Myrmicinae						
Cardiocondyla sp.1	Car1	0	4	3	10	17
Crematogaster sp.1	Cre1	20	27	58	49	154
Crematogaster sp.3	Cre3	0	1	0	0	1
Messor sp.1	Mes1	18	3	60	13	94
Messor capensis (Mayr)	Mcap	51	71	650	75	847
Monomorium sp.1	Mon1	202	0	12	68	282
Monomorium sp.2	Mon2	3	5	8	9	25

(*monomorium* gp)					
Monomorium sp.3 (*monomorium* gp)	Mon3	39	1	0	20	60
Monomorium sp.4	Mon4	1	7	4	0	12
Monomorium sp.5	Mon5	13	0	3	0	16
Monomorium havilandi (Forel)	Mon6	0	0	2	0	2
Monomorium sp.7	Mon7	38	0	2	0	38
Monomorium sp.8 (*salomonis* gp)	Mon8	57	5	10	78	147
Monomorium sp.11	Mon11	0	0	18	0	18
Monomorium sp.13	Mon13	0	0	0	1	1
Ocymyrmex sp.1	Ocy1	1029	6	27	400	1462
Ocymyrmex sp.2	Ocy2	351	10	37	734	1132
Pheidole sp.1	Phe1	785	503	801	687	2776
Pheidole sp.2	Phe2	388	62	224	403	1077
Rhoptromyrmex sp.1	Rho1	6	9	2	0	17
Solenopsis sp.1	Sol1	0	0	1	1	2
Solenopsis sp.2	Sol2	0	0	3	0	3
Tetramorium sp.1	Tet1	57	12	67	99	235
Tetramorium quadrispinosum (Emery)	Tqua	499	56	222	736	1513
Tetramorium frigidum (Arnold)	Tet3	44	2	5	50	101
Tetramorium sp.5 (*simillimum* gp)	Tet5	10	4	5	9	28
Tetramorium sp.7 (*smillimum* gp)	Tet7	94	11	31	60	196
Tetramorium sp.8 (?smillimum gp)	Tet8	4	1	0	5	10
Tetramorium sp.9 (*smillimum* gp)	Tet9	5	1	1	12	19
Tetramorium erectum (Emery)	Tet10	1	0	0	1	2
Tetramorium sp.12	Tet12	0	0	0	1	1
Tetramorium sp.13 (?smillimum gp)	Tet13	1	0	0	1	2
Ponerinae						
Anochetus levaillanti (Emery)	Ano1	1	1	1	1	4
Pachycondyla berthoudi (Forel)	Pber	17	1	9	1	36
Total abundance		5065	1319	6692	12985	26061
Species richness		43	32	42	46	59

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CONSERVATION VALUE OF REMNANTS IN HUMAN-INFLUENCED LANDSCAPES: ANTS IN THE CAPE FLORISTIC REGION LOWLANDS

INTRODUCTION

The global network of protected areas now encompasses in excess of 20 000 reserves, covering a total of 11.5% of the earth's surface (Gaston & Spicer 2004, Rodrigues *et al.* 2004). Nonetheless it has become clear that more is required for the long term survival of species (Rodrigues *et al.* 2004) and increasing importance is being placed on conservation outside of formally protected areas (Knight 1999, Norton 2000, Goodman 2003, Solomon *et al.* 2003, Dudley *et al.* 2005). Since many species occur on or at least have part of their distribution in semi-natural habitats, for example that occur in amongst agricultural and urban areas, these habitats have the potential to greatly enhance long-term conservation success (Pimentel & Stachow 1992, Dudley *et al.* 2005). Among the benefits of successful biodiversity conservation in human-influenced areas are promotion of ecological resilience, increased local diversity in general and enhanced beneficial organisms for biological control of pest species (Duelli & Obrist 2003, Perrings *et al.* 2006).

Current protected area networks have several flaws. One of these is their layout, which is frequently suboptimal for conserving biodiversity. Reserves are often too small to sustain viable populations or poorly sited with little planning to optimize their conservation value (Saunders *et al.* 1991, Reyers *et al.* 2002, Goodman 2003, Gaston & Spicer 2004). Few reserves are placed in areas ideal for long-term survival of species, especially in the face of climate change (Gaston *et al.* 2001, Chown *et al.* 2003, Gaston & Spicer 2004, Opdam & Wascher 2004, Webb *et al.* 2006). Additionally, reserves are often surrounded by land-uses which are incompatible with biodiversity conservation, resulting in alien vegetation and land-use encroachment into reserves (Pimentel & Stachow 1992, Reyers *et al.* 2002).

The possibility of gaining sufficiently more land to increase the conservation status of protected area networks is challenging, if not unfeasible (Chown *et al.* 2003, Perrings *et al.* 2006). Vast amounts of land are continually transformed by agriculture, pollution and resource withdrawal (Bush 1997, Laurance & Cochrane 2001), leaving behind disparate, disturbed habitat patches scattered across the landscape in various

shapes and sizes (Saunders *et al.* 1991, Banks 2000). Indeed the correlated processes of habitat loss and fragmentation are described as the most important ongoing threats to biodiversity (Laurance & Cochrane 2001, Tscharntke *et al.* 2002). Additionally, the increasing and conflicting demand for land by an expanding human population and lack of sufficient funds for conservation initiatives make the establishment of more reserves unlikely (Saunders *et al.* 1991, Reyers *et al.* 1998, Gaston & Spicer 2004). However, conservation outside of protected areas is a viable option, whereby remnants of natural or semi-natural vegetation between agricultural lands and urban areas can provide invaluable links between reserves, greatly enhancing protected area networks (Bush 1997, Farina 2000, Goodman 2003, Gaston & Spicer 2004, Dudley *et al.* 2005).

To successfully conserve natural areas outside of protected areas, it is essential to gain fundamental knowledge of which processes drive and maintain diversity in human-influence landscapes (Parker & Nally 2002, Perrings *et al.* 2006). Human-influenced landscapes are largely characterized by habitat loss, both in terms of quantity and quality and fragmentation of the remaining habitat (Saunders *et al.* 1991, Ovaskainen & Hanski 2003). These processes are known to have negative effects on biodiversity and modify or change ecosystems with regard to their structural and biotic composition as well as functioning (Saunders *et al.* 1991). The severity of the impact of fragmentation on biodiversity depends on several characteristics of habitat fragments such as size, isolation, proportion of edges and habitat quality, as well as characteristics of the surrounding landscape (Bush 1997, Laurance & Cochrane 2001, Perfecto & Vandermeer 2002). These factors influence population abundance and diversity of communities (Laurance & Cochrane 2001, Parker & Nally 2002, Tscharntke *et al.* 2002). Other characteristics of human–influenced landscapes include habitat disturbances, such as pesticides, livestock grazing, invasion of alien species, hydrological changes, changes in fire regimes, and pollutant effects such as acid rain. All of these tend to lead to a degradation of the habitat and may act synergistically with the effects of habitat fragmentation processes (McIntyre & Hobbs 1999, Laurance & Cochrane 2001). Even though remnants are negatively affected by all these processes, human-influenced landscapes remain vital habitats for many species (Kemper *et al.* 1999).

Protecting natural vegetation in agricultural areas has proven to be beneficial for both biodiversity conservation and farming successes. Maintaining remnants of

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natural veld can reduce erosion and benefit hydrological processes (Kemper *et al.* 1999). Additionally, remnants are able to support and enhance predator and parasitoid populations, thereby improving biological control of potential agricultural pest species by preventing large outbreaks (Booij & Noorlander 1992, Bommarco & Ekbom 2000). Most importantly these areas potentially provide a natural reservoir of biodiversity from which disturbed areas can be restored. Natural remnants in agricultural lands are therefore economically important (Kemper *et al.* 1999) and essential to the long-term sustainability of agricultural production systems as biodiversity (Saunders *et al.* 1991, Bestelmeyer & Wiens 1996, Kemper *et al.* 1999, McGeoch 2002, Major *et al.* 2003).

Although the importance of these natural remnants to conservation is well known in theory, in practice they are still poorly understood and the magnitude of the contribution that they play in regional biodiversity conservation is currently unknown. Many species may be able to survive in these remnants simply due to a time delay in their response to the changing environmental conditions, a phenomenon known as extinction debt (Tilman *et al.* 1994). If environmental conditions fall below a threshold required by species for their long term survival, a "debt" is created, which has to be "paid" either by an improvement in environmental conditions or an extinction of the species (Hanski & Ovaskainen 2002). The extinction debt for human-influenced areas is unknown. This information however is vital in determining what needs to be done in these areas to allow for the long-term persistence of species and to develop effective management strategies to maximize biodiversity. At the same time, to further understand human-influenced landscapes, it is important to determine how observed patterns change across spatial scales. Ecological patterns and processes are known to be strongly scale dependent, with patterns observed at local scales being quite different to those observed at regional scale (Lennon *et al.* 2001, Crist *et al.* 2003). Additionally, local scale patterns may be generated by both regional and local-scale processes (Noda 2004). Determining which spatial scale is responsible for generating the greatest variability in biodiversity is important for effective management and conservation strategies (Boyero 2003, Gering *et al.* 2003).

A region that lends itself to study the conservation value of human-influence landscape to the overall conservation of the area, is the Cape Floristic Region (CFR). The CFR is one of the world's 25 biodiversity hotspot, due to its high concentration of endemic taxa, particularly plants and its great vulnerability to processes such as

habitat fragmentation and habitat loss (Myers *et al.* 2000, van Wyk & Smith 2001, Cowling *et al.* 2003). The CFR is situated on the southern tip of Africa and covers an area of about 90 000 km^2 (van Wyk & Smith 2001). The region is extensively transformed, currently 30 % of the total area and continues to be increasingly threatened by factors such as urban development, (currently transforming 1.6 % of the area), agriculture (25.9 %) and dense stands of alien plant invasions (1.6 %) (van Wyk & Smith 2001, Rouget *et al.* 2003). Other contributing factors, which are less easily defined, are unsustainable harvesting of natural resources, such as wild flowers and mining and quarrying activities as well as poor grazing practices (van Wyk & Smith 2001, Rouget *et al.* 2003). Transformation of the region is not evenly spread across the CFR, with low-lying mesic areas having received the greatest impacts. In areas such as Sand Plain Fynbos, more than 50 % has been lost due to urbanization and less than 20 % of Coastal Renosterveld remains due to the impacts of agriculture (Rouget *et al.* 2003). Protected areas are not evenly distributed across the region, with up to 90 % of the mountain fynbos protected in nature reserves and mountain catchment areas, however less than 3 % of the easier accessible lowland fynbos and renosterveld are formally protected (van Wyk & Smith 2001). It is clear that in such areas available habitat is less than that required for any long-term conservation target (Rouget *et al.* 2003). As the land value is high in most parts of the CFR and is also highly fragmented, establishment of new formal reserves is mostly unachievable (Fairbanks *et al.* 2004). Hence involving landowners, especially farmers outside of protected areas, to manage and protect remnants on their land, appears to be the only option for achieving conservation targets for low lying regions of the CFR (Kemper *et al.* 1999, Cowling *et al.* 2003, Fairbanks *et al.* 2004).

Research in the CFR has focused mainly on the plant diversity, however comparatively little is known about the arthropod assemblages (Picker & Samways 1996, Visser et al. 1999, Giliomee 2003). Arthropods are an integral part of ecosystems (Major et al. 2003), regulating many essential ecosystem processes, such as maintaining plant community composition, improving soil structure, nutrient cycling, pollination, seed dispersal and preying on other animals, thereby keeping their populations under control (Majer & Nichols 1998). Little is known about the effects of anthropogenic transformed landscapes on the structure and functioning of arthropod communities in the CFR (Picker & Samways 1996, Donaldson *et al.* 2003, Major *et al.* 2003), although it has been shown that insects in general are sensitive to

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ecosystem changes or disruption (Magagula 2003), especially to vegetation cover, which in turn influences microclimate conditions (Donaldson *et al.* 2003). Although the diversity of arthropods and particularly herbivorous insects is thought to be low in the CFR compared to the high plant diversity (see Giliomee 2003 for possible reasons for this) arthropods play an important role in the CFR. An example of this is the dispersal of seed by ants, termed myrmecochory. A great proportion of plant species in the CFR, around 20 % according to Bond & Silingsby (1983) or 1 300 taxa (Johnson 1992) are known to rely on ants for seed dispersal. The seeds produced by myrmechorous plants have detachable protrusions on their surfaces (elaiosomes), which are high in lipids and fatty acids and contain some proteins. The seeds are carried to ant nests and left underground to germinate there, while the elaiosomes are eaten (Speight *et al.* 1999, Giliomee 2003).

Ants are an appropriate taxon for studies of arthropod diversity in the CFR as they dominate the epigaeic fauna (see Chapter 2). Additionally, ants are well studied and frequently used as indicators in studies assessing impacts of management practices, habitat disturbances and rehabilitation successes (Underwood & Fisher 2006). The ant diversity in the CFR is thought to be relatively poor, with an estimated 100 species occurring in the region (Giliomee 2003). This is comparable to the Californian chapparal and other Mediterranean areas, although southern Australia has a much higher (about 10 times) species richness (Koen & Breytenbach 1988, Giliomee 2003). Ants are also known to be common in agricultural areas of the CFR. In vineyards they are considered pest, as they tend mealybugs which cause considerable damage to vines (Addison & Samways 2000).

The objectives of this study were therefore, 1) to determine the current contribution of remnants in human-influenced areas to the overall conservation of the lowlands of the Cape Floristic Region using ground-foraging ants as the target taxon (i.e. is there a difference in the abundance, species richness, species composition and or functional groupings of ant assemblages in reserves and in adjacent remnant sites in human-influenced areas?), 2) which environmental variables explain ant assemblage patterns, and 3) what is the effect of spatial scale on the differences between ant assemblages of reserve and remnant sites, and which spatial scale is most responsible for generating ant diversity in the CFR lowlands, i.e. the change in ant diversity across areas of increasing extent.

MATERIAL AND METHODS

Study site and design

This study was conducted in the lowlands of the Cape Floristic Region, Western Cape Province. A nested hierarchical structure was used with 5 levels, region, localities, sites, grids and pitfalls. The region was taken as the CFR lowlands and within the region five localities were chosen. Each locality contained two sites (pairs), one a nature reserve and the other an adjacent or near-by remnant site in an agricultural area. Within each site, five independent grids were chosen, approximately 200 - 500 m apart. Finally within each grid there were 10 pitfalls. Appendix 1 gives the localities, study sites and grids and Fig. 1 a map (Appendix 8 shows photos of each grid).

Pitfalls were dug into the ground, in a cross-array with pitfalls spaced 10 m apart (Fig. 2), according to the design suggested by Perner & Schueler (2004). However in one of the localities (Elandskloofberge sites, see below), pitfalls were dug in a 2 x 5 grid (pitfalls 10 m apart) to allow results to be compared to previous studies conducted there (Fig. 2).

Sites were selected so as to represent some of the heterogeneity of the region. All sites were at an altitude below 400 m.a.s.l.. Although the aim was to use remnants adjacent to reserves, this was not always practically feasible, so remnant sites were chosen as close to reserves as possible. Remnant sites selected were placed on farms, where owners/managers have shown an interest in conservation and have either joined conservancies and/or in-cooperated some measures of conservation into their agricultural management practices. The traditional approach to fragmentation, including size and shape of remnants, distance to nearest mainland, and distance between remnants was not adopted in this study due to the landscape complexity and absence of distinct remnants boundaries in the CFR.

The most northern locality was Elandskloofberge (EB). The reserve site was situated in the Elandsberg Private Nature Reserve. This 3900 ha reserve was proclaimed in 1973 and protects the largest remaining unploughed lowland area of two critically endangered vegetation types, namely Swartland Alluvium Fynbos and Swartland Shale Renosterveld (Midoko-Iponga 2004, Mucina & Rutherford 2004). The remnant site was situated in the neighbouring farmland, with remnants lying between wheat fields and cattle and sheep grazed areas. Farming practices include

merino sheep, cattle, wheat, oats, barley, canola, lupines, clover and other feed- crops (Midoko-Iponga 2004). Two of the remnants were exposed to cattle and sheep grazing although relatively intact natural vegetation remained. A further two were situated on old fields and the final remnant was in a vlei area surrounded by wheat fields.

The second most northerly locality was Malmesbury (MB). Riverlands Nature Reserve was selected as the reserve site for this locality. This reserve is approximately 1000 ha and is thought to protect the highest number of plants classified as Red Data Species of any Western Cape Province nature reserve. It is currently the only reserve (besides a few natural heritage sites) protecting the critically endangered Sand Plain Fynbos vegetation type (68) of which less than 1.05 % is conserved (Rebelo 2006). It is however largely surrounded by alien vegetation. The remnant site in this case was taken as Pella Nature Reserve. It is in essence one large remnant (269 ha) surrounded by farmland, heavily invaded by alien vegetation (Jarman & Mustart 1988). This area was subject to frequent fires pre-1960 and since then has been used as natural grazing for livestock (Brownlie & Mustart 1988). However, this has stopped in the recent past and no livestock grazing occurred in Pella Nature Reserve during the sampling period. The natural vegetation appeared to be pristine.

In the Grabouw (GR) locality, the reserve site was situated in the Hottentots-Holland Nature Reserve. This reserve (about 42 000 ha) is mountainous with altitudes reaching up to 1590 m and is important in conserving mountain fynbos (CapeNature 2006). Sampling grids in the reserve were situated in the lower lying areas between the mountains and the Theewaterskloofdam. In this locality the reserve and remnant site were situated about 23 km apart. The GW remnant site was situated on a farm under various farming practices, with vineyards and orchards being the main focus. Orchards include apples, pears and plums. The farm forms part of the Groenlandberg Conservancy, which covers an area of about 34 000 ha and stretches from the Grabouw/Elgin Valley to Botrivier and across to the Hottentots Holland Reserve (IUCN 2006). It is also a member of the Biodiversity and Wine Initiative, a partnership between South Africa wine industry and the conservation sector (Anonymous 2006). All the remnants were heavily invaded by alien vegetation. One remnant was placed in an area cleared of alien trees about a year or two prior to sampling and another was subject to trampling by antelope.

Jonkershoek Nature Reserve was chosen as the reserve site in the Stellenbosch (STB) locality. The reserve, about 9800 ha in extent, includes the Jonkershoek Mountains and part of the upper Jonkershoek valley and is an important water catchment area. A number of the known 1100 plant species in the reserve are endemic and or rare (CapeNature 2006). The corresponding remnant site in the locality was about 24 km away, on a wine farm. The farm is situated on the edge of the Bottelary Hills Conservancy (Anonymous 2002). Remnants were relatively undisturbed. However, a frequently used 4 x 4 track runs through the natural area containing the remnants and surrounding areas were intensely utilized. The vegetation in the remnants was relatively old and moribund and occasionally alien invasive plants were present.

The final locality was Somerset West. The Municipal Helderberg Nature Reserve was chosen as the reserve site. This reserve, around 380 ha in size, is the smallest of the ones selected, and encompasses the Helderberg Mountain (HelderbergNatureReserve 2006). Parts of the reserve were and in some places still are under alien tree plantations. The remnant site was situated on the opposite side of the mountain on a wine farm with a keen interest in conservation. One remnant was situated in an old vineyard, where natural vegetation had been planted. Another remnant was located at the edge of a large sheep enclosure and a further one was severely invaded by alien vegetation. The remaining two remnants were largely undisturbed.

Abiotic variables

For each grid, GPS readings were taken using a GARMIN GPS and aspect and slope (a qualitative scale was used) were recorded. Climate data for each site, including rainfall, wind speed and relative humidity, from adjacent weather stations were obtained from AgroMet – Institute for Soil, Climate and Water (ISCW) as well as the Water Research Commission (WRC), Council of Scientific and Industrial Research (CSIR) and Western Cape Nature Conservation Board (WCNCB). Weather data for both the 5 - day sampling period as well as means across 2004 were used. The ground temperature for each grid was measured during the five day trapping period. This was done by inserting two temperature loggers, Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim), roughly in the centre of the grid 2 cm beneath the surface of the soil. Care was taken that temperature loggers were not

placed in heavily shaded areas, unless the grid was also exposed to such conditions. Soil moisture was determined gravimetrically. Samples were dried at 100ºC for a minimum of 48 hours and percentage soil moisture ((wet soil mass – dry soil mass/wet mass)*100) was determined. To determine the nutrient content and particle fraction of the soil, samples from the top 0.5 - 0.10 m soil next to each pitfall were taken with a small shovel to gain a representative soil sample for the plot. The soil was then oven dried at 60 °C and sent to BemLab (Pty Ltd.), South Africa, for testing. The soil samples were analysed for composition (sand, silt, clay), pH (McLean 1982), extractable cations namely K, Na, Ca, Mg (Chapman 1965), extractable phosphorus (Bray & Kurtz 1945), organic carbon (C) (Nelson & Sommers 1982), total nitrogen (N) and soil resistance (R) (STAFF 1954).

Vegetation and litter sampling

Relative percentage vegetation cover around each pitfall was estimated using the following categories: bare soil, litter, grass, herbaceous and woody plants. A quadrat (1 m^2) was placed over the pitfall and the percentage of each category in the square was estimated. Foliage height profiles (FHP) around each pitfall were also measured to determine the vertical complexity of the vegetation (Bestelmeyer & Wiens 1996). A measuring rod was placed at four points 90° apart on a 1 m radius circle with the centre at the pitfall. Measurements were divided into 7 height classes at 0.25 m intervals; starting at a height of 0.25 m and ending at 1.50 m. Plants above 1.50 m were all assigned to the last height class. All parts of the plant that touched the measuring pole, i.e. number of hits, within a certain height class were recorded (Bestelmeyer & Wiens 1996, Bestelmeyer *et al.* 2000, Botes *et al.* 2006). Dominant plant species as well as alien invasives at each plot were recorded. Additionally plants present in each cross-array were identified to determine an estimate of plant species richness per grid (det. B. Walton).

While retrieving pitfalls at the end of the 5 - day period, litter samples were taken. Three 0.1 m^2 square sampling grids were randomly placed around each pitfall and all dead plant material within the three squares was collected and placed into separate brown paper bags. These were oven dried at 60 ºC for a minimum of 72 hours. The dried litter was sieved using a sieve (4 mm diameter circular holes) to separate litter into coarse and fine material which were then weighed separately.

Ant sampling

Sampling was conducted in late spring (October 2004), which falls within the peak activity and biomass period for ants in the Cape Floristic Region (Schlettwein & Giliomee 1987, Johnson 1992b). Pitfalls traps, plastic containers (150 ml, 55 mm diameter, 70 mm deep) with screw-on caps, were used. These were dug in level with the surrounding soil surface. The pitfalls remained covered for at least five days, to reduce the "digging-in effect" (Greenslade 1973, Abensperg-Traun & Steven 1995, Southwood & Hendersen 2000), after which they were opened for a period of five days. To set the traps 50 ml of a 50 % propylene glycol solution was poured into the opened pitfalls (Bestelmeyer *et al.* 2000). This preservative is non-toxic to vertebrates (Bestelmeyer *et al.* 2000), and neither attracts or repels ants (Abensperg-Traun & Steven 1995). Pitfalls within a site were set and removed in the same order over as short a period as possible, typically between 10h00-15h00, to ensure that they were open for equal lengths of time. The two sites in a region were sampled during the same five day period were possible (otherwise a day apart), to reduce the effects of weather on paired sites. The pitfall contents were washed and preserved in 70 % alcohol.

The fauna were identified under a Leica-M Series Stereo-microscope. The ants (Hymenoptera: Formicidae) were identified to genus and species level where possible, or assigned to morphospecies. For each ant species collected voucher specimens are held at the University of Stellenbosch.

Data analyses

Environmental data

Weather (rainfall, relative % humidity, wind speed and ground temperature), soil (% moisture content, nutrient concentrations, particle composition and pH) and vegetation (% vegetation cover, foliage height profiles and litter) data were summarised per site and, where sufficiently detailed data was available, per grid. Variables were compared statistically across sites using non-parametric Kruskal-Wallis tests and post-hoc, multiple comparisons of mean ranks for all groups, tests. Mean, maximum and minimum ground temperature data were further analysed by taking four readings per day, 0h00, 6h00, 12h00 and 18h00 and comparing these across sites using one-way ANOVA.

Due to the large number of environmental variables, principal component analysis (PCA) was used to reduce variables to fewer principal component axes. This method allows one to include all environmental variables so that even variables which appear to be weak, but potentially biologically important are included. Resultant axes are able to adequately summarize the original information and are un-correlated and independent of each other (Quinn & Keough 2002). PCA's were run for three groups of variables, namely climate, soil and vegetation, and for all variables together. Since the former gave results which were easier to interpret than those of a single PCA including all variables, it was decided to use the PCA's for each of the three explanatory groups. To aid the interpretation of the PCA axes (see Vaughan & Ormerod (2005)) prior to the PCA, variable clustering was conducted to group data more effectively. Agglomerative hierarchical cluster analyses, however, did not produce more meaningful clusters that those selected (i.e. soil, climate and vegetation) and hence this method was omitted.

Initially, another method for reducing variables based on Botes *et al.* (2006) was used, where collinearity in variables was determined using Spearman's correlations. Variables were again divided into three groups, climate, soil and vegetation. In each case, where variables were significantly correlated (and with $r_s > 0.7$), one of the two was excluded based on the presumed biological relevance. This method however only reduced the 52 variables to 16 (in the case of site scale variables) across all three groups compared, while the PCA method reduced information to less than 12 variables. Hence the latter method was used. Determining which axes to use for subsequent analyses was done based on a broken-stick method (Legendre & Legendre 1998, Peres-Neto *et al.* 2003) and/or based on % variance explained by the individual axes.

Ant species richness, abundance & composition

Data from the pitfall traps was pooled into a single sample per grid, so that samples were independent of each other, or grouped together into a single sample per site by pooling grid data. Site data was also summarised into locality (paired sites data). Data were then analysed at three hierarchical levels, using grid data (n = 50 grids), site data (n = 10 sites) and locality data (n = 5 localities, i.e. 5 reserve-remnant pairs). Comparisons were made between reserve and remnants using i) reserve grids (n = 25 grids) vs. remnant grids (n = 25 grids), ii) pooled reserve grids (5 sites) vs.

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pooled remnant grids (n = 5 sites) and iii) for each locality, reserve (n = 5 grids) vs. remnant (n = 5 grids). Additionally, comparisons were made between i) sites (n = 10 sites) and ii) between localities (n = 5 localities) across the region.

To determine if sampling effort was adequate, sample-based rarefaction curves were compiled using grid data for each site, each region and for all sites together using EstimateS V7.5, Colwell 2000, http://viceroy.eeb.uconn.edu/etsimates. Sample-based rarefaction curves compare species density, i.e. number of species per unit area, of the different sites and localities (Gotelli & Colwell 2001). To compare species richness of various sites and localities, sample-based rarefaction curves were re-scaled to individuals, i.e. curves were compiled plotting species richness against number of individuals for the sites, localities and overall area (Gotelli & Colwell 2001).

Species richness estimators, calculated by EstimateS (with replacement) were used, to determine the predicted species richness of each site, locality and the total area. There are a host of different species richness estimators each with a different accuracy, i.e. combination of precision and bias (Walther & Moore 2005). Due to the incongruence in the literature as well as recommendations to use several estimators rather than a single one, we decided to use four different non-parametric estimators based on incidence-values only (Hortal *et al.* 2006). Abundance data for ants is problematic, as ants are social insects and their distribution is aggregated in space. Samples from pitfall traps may therefore result in an extreme abundance of an otherwise rare ant in the assemblage being caught (Lobry DeBruyn 1993, Longino 2000, Leponce *et al.* 2004). Hence using presence/absence incidence data is more reliable than abundance data for ant species (Bestelmeyer & Wiens 2001). Four incidence-based estimator, ICE, Jack1 & 2 and Chao2, were thus used. Although non-parametric species richness estimators are known to have drawbacks and potential inaccuracies, they nonetheless provide useful information of at least a minimum estimate of true species richness in areas were no inventories are available (Longino *et al.* 2002, O'Hara 2005, Hortal *et al.* 2006).

Shared species were calculated between localities and between paired reserve and remnant sites in a locality, using observed values. SPADE, Species Prediction And Diversity Estimation program (Chao *et al.* 2000, Chao & Shen (2003-2005)) was used to determine the estimated number of species shared.

Rank abundance and occupancy distributions were constructed for sites and the overall data set, using both abundance and occupancy data (calculated from

presence/absence in pitfalls). Although, as previously mentioned, abundance data is problematic, occupancy data is only logical for individual species occurrence in traps and not for the collective abundance of ants. Hence both abundance and occupancy were used for analyses, but where occupancy simply reduced to species richness, only abundance data was used.

To determine which species were characteristic of reserve and remnants, as well as individual localities and sites, indicator values were determined using the Indicator Value Method, proposed by Dufrêne & Legendre (1997). This method combines specificity (the uniqueness of a species at a site) with the fidelity (frequency at that site) and then provides an Indicator Value (IndVal) as a percentage for each species. High values indicate that the species is characteristic of the site, with species having significant values above 70 % regarded as a benchmark for indicator species (van Rensburg *et al.* 1999, McGeoch *et al.* 2002). Indicator species were determined for combined reserve and remnant sites, individual sites and localities.

The ant genera were assigned to functional groups following Andersen (1995) to determine compositional differences between reserve and remnant ant assemblages. Functional groups included, Dominant Dolichoderinae (generally abundant, active and aggressive), Sub-ordinate Camponotini (co-occur but behaviourally submissive to Dominant Dolichoderinae), Hot Climate Specialists (adapted to arid environments), Tropical Climate Specialists (distribution mainly in humid tropics, occur where Dominant Dolichoderinae is not abundant), Cryptic Species (small body size, predominantly forage in soil and litter), Opportunists (unspecialized species, characteristic of disturbed sites, or other habitats supporting low ant diversity), Generalized Myrmicinae (ubiquitous, highly competitive taxa occurring in most habitats) and Specialist Predators (specialized diet, large body size and small colony size) (Andersen 1997a, Hoffmann & Andersen 2003).

Analysis of Similarity (ANOSIM, 1000 permutations), using the Bray-Curtis similarity measure, was performed in PRIMER v 5.0 (Clarke & Gorley 2001), to determine whether there was a significant difference between the ant assemblage structures of reserve and remnant paired sites. Data were fourth root transformed and standardised prior to analysis so as to reduce the contribution made by more common species to the similarity measure (Clarke & Gorley 2001).

Environmental determinants of ant assemblages

To determine the proportion of variation in ant species richness and abundance explained by spatial and environmental variables, trend surface analysis and partial regression approaches were used following Legendre & Legendre (1998), with the exception of using generalized linear rather than least-squares models (see McGoech & Price (2004)). Generalized Linear Models (GLZ) assuming a Poisson error distribution (log-link function, Type III model: Dobson 2002) were performed using pooled grids within sites (n = 10), individual grids (n = 50) and locality data (n = 5) separately.

Trend surface analysis was performed to determine the best-fit combination of spatial variables that contributed significantly to explaining the variation in the dependent variables. A third order polynomial of the longitude and latitude records of the sites/grids was used as a model for the spatial component of the variation in species richness and abundance, as this extracts linear as well as more complex features from the data (following Legendre & Legendre (1998)). Multiple regression (ordinary least squares) were used, and abundance data were log_{10}-transformed to improve data distribution, while species richness data were left untransformed. Initially, GLZ's (maximum likelihood) were run, however most likely due to too few degrees of freedom, the log-likelihood could not be maximised and hence GLZ results were not used. Parameter estimates for the abundance models were corrected for over dispersion in the residual deviance (Dobson 2002).

Generalized Linear Models were then performed for the environmental variables on ant species richness and abundance. Instead of using individual environmental variables, PCA axes were used. For the combined site and grid models, all four PCA axes for each of the climate, vegetation and soil PCA's were used. For the locality level models, only the first axes were used for each climate, vegetation and soil variable PCA. Initially, individual environmental terms were included in the GLZ. However the individual variable combinations always explained less of the variability in the dependent variable than the PCA axes, therefore the PCA axes were used. The best subset of PCA axes were selected as the significant model with the fewest terms (although one of each climate, vegetation and soil PCA axes was kept in the sites and grid models) and lowest deviance. Analysis of deviance was conducted to determine significant differences between models, whereby the critical χ^2 value on

the difference in the degrees of freedom and deviance between the models was used (McCullagh & Nelder 1989).

Initially the proportion of variation in estimates of species richness and abundance (Jack 2 species richness estimator and number of individuals estimated by EstimateS), explained by environmental and spatial variables at the site level were also analysed. However, since observed species richness and Jack 2 values gave similar results, as did observed and estimated number of individuals, only observed species richness and abundance results are shown.

Canonical Correspondence Analysis (CCA) (CANOCO v4.5: ter Braak & Šmilauer (2002)) was used to determine the response of ant assemblages to gradients in the environmental variables. This analysis was selected after examination of Direct Gradient Analysis (DCA) gradient lengths (Lepš & Šmilauer 2003). CCA is a form of multivariate, direct gradient analysis, where axes extracted are constrained to be linear combinations of the variables measured (ter Braak & Šmilauer 2002). Grid data was used for the analysis and the species data was $\log_{10}$-transformed prior to analysis. A forward selection procedure of environmental data was then used to determine which of the variables significantly explained ant assemblage structure. The significance of the variables was tested using a Monte Carlo simulation (1000 permutations). CCA ordination results were given as biplots using the first two canonical axes, where significant environmental variables are depicted as arrows and sites as symbols (Lepš & Šmilauer 2003). The lengths of the arrows indicate the relative importance of the individual environmental variables in explaining species composition. The direction of the arrows indicates the direction of the steepest increase of the contribution (Lepš & Šmilauer 2003). Biplots of the samples (sites) and species were also plotted, to investigate which species contributed most to the assemblage structure. Only ants which had more than 30 % of their variability explained by the ordination subspace were shown. Finally, the CCA with environmental variables was repeated, but the invasive Argentine ant (*Linepithema humile*) was excluded from the ant species data and included as an environmental variable, as a presence or absence of the Argentine ant. Again a forward selection procedure was used to determine which of the variables significantly explained ant assemblage structure (now excluding the Argentine ant) and the results were plotted on a biplot similar to the initial CCA with environmental variables.

Beta diversity

Beta-diversity was calculated using two methods. The first is based on the additive partitioning of diversity, where regional diversity (γ) = local diversity (α) + beta diversity (β) (Lande 1996). In this study observed species richness was used as a diversity measure. For each level i, β_i was calculated as $\alpha_{i+1} - \alpha_1$, where α_1 is the mean species richness found in samples at that level. Therefore, beta-diversity for the additive approach is the average number of species absent from a sample at a certain level (Veech *et al.* 2002) or the difference in species richness of a level and the average species richness found in the next lowest level. Mean beta diversity was calculated for each nested hierarchical level, pitfalls, grids, sites, localities and overall region. Total additive partitioning of species richness across the region was therefore given by $\gamma = \alpha_{pitfalls} + \beta_{pitfalls} + \beta_{grids} + \beta_{sites} + \beta_{localities}$ and $\gamma = \alpha_{pitfalls} + \beta_{pitfalls} + \beta_{grids} + \beta_{sites}$ for reserve and remnants additive partitioning. Note that for example $\alpha_{grids} = \alpha_{pitfalls} + \beta_{pitfalls}$ (Veech *et al.* 2002, Crist *et al.* 2003, Gering *et al.* 2003).

The observed beta diversities of the various levels were compared to null models at each level, to determine whether observed values differed significantly from those expected by chance. The computer program, PARTITION (Gering & Crist 2002, Veech *et al.* 2002, Crist *et al.* 2003) was used. This program calculates expected values for each sampling level, by randomly allocating the next lowest level's samples within those of the next higher sampling level, e.g. to determine expected alpha and beta diversity at the grid level, pitfalls are randomly allocated to grids within the same site. Probability values (p values), which are the proportion of randomized data sets that are greater or less than the observed are also calculated, e.g. if 6 out of 1000 randomizations are greater than the observed, the probability of obtaining an estimate greater than the observed value by chance is 0.006 (Crist *et al.* 2003, Summerville *et al.* 2003). In this study, four separate randomization events (10 000 randomizations) were conducted. Individual-based randomization, randomly allocating individuals to pitfalls that belong to the same grid, was used to determine expected species richness values at the pitfall level. For grids and sites, sample-based randomization was used, whereby grids were randomly allocated within sites, sites were randomly allocated within localities and sites were randomly allocated within the region. Species abundance and sample-size distribution are maintained so that even though each randomization produces different number of species in individual

samples, overall species richness across each hierarchical level remains the same as the observed data (Summerville *et al.* 2003).

The second method is based on the multiplicative partitioning of diversity, where γ = α x β. The β_{sim} measure was used (Lennon *et al.* 2001),

$$\beta_{sim} = \frac{1}{n}\sum_{i=1}^{n}(1-S_i); S_i = \frac{a_i}{a_i + \min(b_i, c_i)} ,$$ where *a* is the number of species shared

between two quadrates, *b* is the number of species present in only the neighbouring quadrate and *c* the number of species in only the focal quadrate. This measure provides a direct assessment of turnover in species composition, measuring species gains and losses (Koleff *et al.* 2003). β_{sim} was also calculated for all hierarchical levels. This was done by calculating the mean β_{sim} value between pitfalls for each grid first (from a, b and c values for each pair of pitfalls from that specific grid) and then averaged across the 50 grids. For between grids, β_{sim} was calculated for each grid within a site first (from *a, b* and *c* values for each pair of grids within a site), and then averaged across all 10 sites. This was then also done for between paired sites of localities and between sites within the region and between localities within the region. General linear models were used to determine significant differences between hierarchical levels and reserve and remnant. Due to the large number of data points for β $_{sim}$ for pitfalls in relation to those of grids and sites, only 50 data points were selected randomly for each site. The Factorial ANOVA showed level to be significant, while reserve/remnant was not significant and hence a model including only level was used.

RESULTS

Environmental variables
Between reserve and remnants

There were no significant differences in weather variables between the reserve and remnant paired sites within each locality (referred to as between pairs from now on) (Appendix 2A - C). There were however significant differences in soil variables between pairs (Appendix 3A - E). These were restricted to the Grabouw and Stellenbosch localities. At the Grabouw locality, the remnant site had significantly higher clay (Kruskal-Wallis test, H = 35.96, d.f. = 49, p < 0.001) and silt content (Kruskal Wallis test, H = 36.63, d.f. = 49, p < 0.01) and significantly lower sand

content (Kruskal Wallis test, H = 41.97, d.f. = 49, $p < 0.001$) (Appendix 3B). The soil of the Grabouw reserve site was significantly more acidic (Kruskal Wallis test, H = 33.63, d.f. = 49, $p < 0.01$) (Appendix 3C) and had a significantly higher soil resistance than that of the remnant site (Kruskal Wallis test, H = 38.74, d.f. = 49, $p < 0.001$) (Appendix 3A). The Grabouw reserve site also had significantly lower exchangeable cations (Ca, Mg, Na, K) (Kruskal Wallis tests, d.f. = 49, $H_{Ca} = 42.16$, $p < 0.001$, $H_{Mg} = 43.88$, $p < 0.001$, $H_{Na} = 36.13$, $p < 0.001$, $H_K = 42.94$, $p < 0.001$) and % base saturation (Mg and Na) (Kruskal Wallis tests, d.f. = 49, $H_{Mg} = 40.08$, $p < 0.001$, $H_{Na} = 26.15$, $p < 0.01$) than the remnant site (Appendix 3A). The Stellenbosch remnant site had significantly higher % base saturation (Ca) than the reserve site (Kruskal Wallis test, H = 33.82, d.f. = 49, $p < 0.001$) (Appendix 3A).

There were no significant differences between pairs for vegetation cover (Appendix 4A). However, the foliage height profile at the Stellenbosch locality showed a significant difference in foliage density between pairs at the below 0.25 m category (Kruskal-Wallis test, H = 28.16, d.f. = 49, $p < 0.001$) (Appendix 4B). There were also no differences in the amount of litter collected, both coarse and fine between pairs (Appendix 4 C).

In summary, only two pairs had significant differences in environmental variables measures. In the Grabouw pair, soil variables were mainly different, while in the Stellenbosch pair there was a difference in a single soil and single vegetation variable.

Between sites

There were significant differences across sites for the majority of the environmental variables (Appendix 2A – 4C). The Elandskloofberge sites received the highest rainfall during the five-day sampling period, while the Somerset West remnant site received no rain during the sampling period (Appendix 2A). Ground temperatures were highest in the Malmesbury sites (Appendix 2B & 2C) and significantly so compared to all other sites at 12h00 and 18h00 (ANOVA, $F_{1,9} = 20.86$, $p < 0.001$ and ANOVA, $F_{1,9} = 17.27$, $p < 0.001$ respectively). Significant differences were also found between sites at 6h00 (ANOVA $F_{1,9} = 3.99$, $p < 0.001$) and 0h00 (ANOVA, $F_{1,9} = 8.84$, $p < 0.001$) (Appendix 2C).

All soil characteristics differed across sites (Appendix 3A - E). The Grabouw remnant site had loam soil, while the other sites had predominantly sandy soils. The

component of clay, soil and silt differed significantly across the sites (Appendix 3B) (Kruskal-Wallis test, H_{clay} = 35.96, d.f. = 49, p < 0.001, H_{silt} = 36.63, d.f. = 49, p < 0.01 and H_{sand} = 41.97, d.f. = 49, p < 0.001). The acidity (pH) differed across sites (Kruskal Wallis test, H = 39.45, d.f. = 49, p < 0.001) (Appendix 3C). The Somerset West sites had significantly higher soil moisture content than those of the Malmesbury sites (Kruskal Wallis test, H = 39.45, d.f. = 49, p < 0.001) (Appendix 3D). T-value, which is an estimate of the cation exchange capacity (CEC) value, was significantly different across sites (Kruskal Wallis test, H = 43.87, d.f. = 49, p < 0.001) (Appendix 3E). Cation exchange capacities for Na, K, Ca and Mg and (Kruskal Wallis tests, d.f. = 49, H_{Na} = 36.13, p < 0.001, H_K = 42.94, p < 0.001 H_{Ca} = 42.16, p < 0.001, H_{Mg} = 43.88, p < 0.001) and % base saturation for Na, K, Ca and Mg also differed significantly across sites (Appendix 3A) (Kruskal Wallis tests, d.f. = 49, H_{Na} = 26.15, p < 0.01, H_K = 27.36, p < 0.01, H_{Ca} = 33.82, p < 0.001, H_{Mg} = 40.08, p < 0.001). The following soil variables also differed across sites, soil resistance (Kruskal Wallis test, H = 38.74, d.f. = 49, p < 0.001), H^+ concentration (Kruskal Wallis test, H = 33.14, d.f. = 49, p < 0.001), % N (Kruskal Wallis test, H = 39.75, d.f. = 49, p < 0.001), and % C (Kruskal Wallis test, H = 38.34, d.f. = 49, p < 0.001) (Appendix 3A).

Percentage vegetation cover was significantly different between sites for all categories, bare ground, (Kruskal Wallis test, H = 18.63, d.f. = 49, p < 0.05), litter (Kruskal Wallis test, H = 28.82, d.f. = 49, p < 0.001), grass (Kruskal Wallis test, H = 20.45, d.f. = 49, p < 0.05), herbaceous component (Kruskal Wallis test, H = 31.17, d.f. = 49, p < 0.001) and woody vegetation (Kruskal Wallis test, H = 27.94, d.f .= 49, p < 0.05) (Appendix 4A). Foliage height densities differed significantly for the lower categories 0 - 0.25 m (Kruskal Wallis, $H_{9,50}$ = 28.16, p < 0.001), 0.25 - 0.50 m (Kruskal Wallis, $H_{9,50}$ = 17.38, p = 0.04), 0.50 - 0.75 m (Kruskal Wallis, $H_{9,50}$ = 23.07, p < 0.01) and 0.75 - 0.10 m (Kruskal Wallis, $H_{9,50}$ = 21.57, p = 0.01), but not for the higher classes, 0.10 m – 150 + m.

Mean litter weight, as well as coarse and fine weight per site was also significantly different across sites (ANOVA, $F_{1,9}$ = 4.47, 4.24 and 4.59 respectively, p < 0.001) (Appendix 4 C). Median percentage litter cover was not significantly correlated to mean weight of litter but was significantly positively correlated to the percentage fine weight (total fine weight/ total weight) (r_s = 0.34, p < 0.05). In general there were many significant differences across sites for environmental variables

measured, with a greater difference in environmental variables between sites than between pairs.

Reducing environmental variables

Principal component analysis reduced the environmental variables to four principal components for each category, i.e. climate, vegetation and soil. Using climate site data, the first principal component (PC) captured 30.5 % of the variance and the first two, 51.4 %. The first PC mainly represented an increase in ground temperature (mean, mean maximum, absolute maximum and range) and a decrease in humidity. The second PC mainly represented an increasing rainfall across 2004 gradient and decreasing number of rain days during the five day sampling period and an increasing minimum ground temperature (Appendix 5A & E). Using the grid climate data, 70.6 % of the variation in the climate data was captured by the first PC and 97.4 % by the second PC (Appendix 5F). Using locality data, the first axes explained between 64.1 % (Elandskloofberge) and 79.1 % (Malmesbury) of the variation. The first and second axis combined explained between 96.9 % (Malmesbury) and 99.2 % (Grabouw) (Appendix 5G).

PCA for sites, using vegetation data, the first PC explained 42.9 % of the variance in the vegetation data and the first two PC's explained 64.6 %. The first principle component mainly represented an increasing gradient in litter (mean, coarse and fine and % cover) and foliage density above 0.5 m and a decrease in foliage density below 0.25 m. The second axis represented mainly an increase in plant species richness and % herbaceous component (Appendix 5E). Grid vegetation data PCA results showed the first PC and first two PC's to explain 31.8 and 45.3 % of the variance (Appendix 5F). Using vegetation, locality data the first PC captured between 33.5 % of the variance (Malmesbury) and 46.6 % (Somerset West). The first two axes captured between 58.3 % (Malmesbury) and 70.2 % (Somerset West) (Appendix 5G).

Using soil site data, 65.5 % of the variance was captured by the first PC and 82.3 % by the first two principle axes (Appendix 5E). The loadings on the first PCA axes showed that the axes represented mainly an increasing gradient of soil moisture and nutrients (many soil nutrient variables), clay and silt content and decreasing sand component, while PC2, mainly represents soils with an increasing hydrogen ion concentration. Using grid soil data, PC1 captured 56.4 % of the variance, mainly representing a decreasing gradient of soil nutrient, clay and silt content and increasing

sand component and resistance in the soils (Appendix 5D). The first two PCs together captured 71.7 % of the variance (Appendix 5F). Using individual locality soil data, the first PC captured between 38.7 % of the variance in the case of Malmesbury sites to 74.8 % for Grabouw sites of the variance. The first two PCs together captured from 62.8 % (Malmesbury) to 89 % (Grabouw) of the variation (Appendix 5G).

For vegetation and soil data, where the same variables were used at site and grid level, very similar PCA ordination plots were obtained and therefore only the ones using grid data are shown (Appendix 5C & D). However for climate data, where different variables were used at grid and site level, both ordination plots were given (Appendix 5A & B). Climate variables PCA, using site level data, showed a negative relationship between temperature and humidity. Vegetation variables PCA using grid data, showed a positive relationship between % woody component and foliage density above 0.25 m and mean, coarse and fine litter mass. Soil variables PCA, using grid data, showed a clear positive relationship between % silt and % clay and the concentration of exchangeable cations and % base saturations as well as other nutrients such as carbon, nitrogen and phosphorus.

Ant species richness, abundance and composition

A total of 13 493 ant individuals representing 83 species from 24 genera were collected across the 10 sites. Most species and genera belonged to the subfamily Myrmicinae with 43 species 11 genera, followed by the subfamily Formicinae, with 25 species and four genera. The genus *Monomorium* contained most of the species (15), followed by *Tetramorium* (14) and *Camponotus* (12).

Samples from individual sites, localities and the overall area were representative of the ant fauna expected at sites and across the localities as is indicated by the approximate asymptotes reached by the sample-based rarefaction curves (Fig. 3A). The results of all four species richness estimators generally did not differ markedly from the observed species richness, with Chao2 predicting the highest species richness and Jack1 the lowest (Table 1). Elandskloofberge and Stellenbosch reserves and Malmesbury remnant site had the greatest difference between observed and predicted species richness estimated, with estimates predicting an increase of 18, 16 and 12 % in the species richness respectively (Chao2) (Table 1).

Assemblages in sites and localities all showed a clear numerical dominance structure. Dominance ranged from around 90 % (*Anoplolepis steingroeveri* in

Elandskloofberge reserve site) to less than 30 % (*Linepithema humile* in the Somerset West sites) (Fig. 4A). Overall *A. steingroeveri* was the numerically most abundant ant species, however *Tetramorium quadrispinosum* had the highest occupancy, occurring in all sites (Fig. 4A & B, see also Appendix 6). The invasive Argentine ant (*Linepithema humile*) was the second most abundant species trapped, although it was only found at 5 sites. The species dominated in the Somerset West sites, as well as in the Grabouw remnant site. Sites where the Argentine ant was present, had a significantly lower species richness than those where it was absent, when using grids level data (ANOVA $F_{1,1} = 4.95$, $p < 0.05$). Of the 82 other species, 24 only occurred at sites where the Argentine was not present (Appendix 6), such as *Anoplolepis custodiens* and 37 species only occurred at grids where the Argentine ant was absent.

Between reserve and remnants

In the pooled reserves 69 species were captured and 66 species in the combined remnants (Appendix 6, Table 1). There was no significant difference in observed species richness between pooled reserve and pooled remnant sites (GLM, $F_{1,48} = 2.02$, $p > 0.05$). Species richness estimates for pooled reserve sites and pooled remnant sites were also not significantly different (Wilcoxon Matched pairs Test, T = 4.00, Z = 0.94, p = 0.34, N = 5). However, significant differences were found between estimates (using Jack 2) of species richness between pairs for Elandskloofberge (t = 2.029, d.f. = 24, p < 0.05), Grabouw (t = 2.834, d.f. = 24, p < 0.05) and Stellenbosch (t = 2.183, d.f. = 24, p < 0.05), but not between pairs of Malmesbury and Somerset West localities (p > 0.05). Individual-based as well as sample-based rarefaction curves revealed species richness of reserve sites to be higher than the corresponding paired site, except for the Elandskloofberge sites, where the opposite was true (Fig. 3B).

Of the 83 species observed, 63 % were observed in both reserves and remnants, 17 occurred only in reserves and 14 only in remnants. Of those only 4 occurred in more than one reserve site and only 3 occurred in more than one remnant site (Appendix 6). Reserve and remnant sites shared the highest percentage of species in the Elandskloofberge locality and the lowest in the Stellenbosch locality. Estimated number of species shared was very similar to that observed for all localities, except Elandskloofberge and Somerset West, which had an estimated seven species more shared than observed (Table 2).

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No indicator species were found for combined reserves, however for the remnants, the Argentine ant was noted (Table 4). Although this species is not an indicator species by definition of the subjective benchmark, it was the only species with an significant indicator value above 50. The next highest indicator value was *Meranoplus peringueyi* with 29.9, which was not significant.

Grouping species into functional groups, using species richness data, showed little difference between reserve and remnant sites, except that no Tropical Climate Specialist (TCS) were found in remnant sites (Fig. 5A). The greatest proportion of species were Opportunist Species (OPP) for both reserves and remnants (Fig. 5A). Relative abundance was markedly different between reserve and remnants, with reserves having a higher proportional abundance of Hot Climate Specialists (HCS) and a proportionally lower abundance of Generalized Myrmicinae (GM), Dominant Dolichoderinae (DD) and Opportunist Species (Fig. 5B). These results are however biased by the overwhelming abundance (4050 individuals) of *Anoplolepis steingroeveri* in a single reserve grid. This species contributed heavily to the large proportion of Hot Climate Specialists (HCS) in reserves.

Differences in ant assemblage structures between pooled reserve and pooled remnant sites, although significant, were very weak (low R-value) (Global R = 0.071, p = 0.03) and assemblages could not be clearly separated (Clarke & Gorley 2001). For individual localities, ant assemblage structure differed significantly between pairs in Grabouw (Global R = 0.916, p < 0.05), Stellenbosch (Global R = 0.864, p < 0.05) and Malmesbury (Global R = 0.852, p < 0.05), but not between the Elandskloofberge (Global R = 0.02, p = 0.44), and Somerset West pairs (Global R = 0.176, p = 0.08).

In summary, ant assemblages showed no overall differences between reserves and remnants, in terms of species richness, abundance, composition and only very weak differences between assemblage structures. Some individual pairs however had significant differences between ant species richness, composition and assemblage structure.

Between sites and localities

Observed species richness and number of individuals differed significantly between sites (Kruskal Wallis test, H = 20.98, d.f. = 9, p < 0.05 and H = 22.40, d.f. = 9, p < 0.05). The Elandskloofberge reserve site had the highest number of individuals (4601), while the Elandskloofberge remnant site had the highest species richness (36)

(Table 1). The Somerset West remnant site had both the lowest number of individuals (447) and species (18) (Table 1). Grabouw and Stellenbosch localities shared the highest % of species (48.39), while Malmesbury and Somerset West shared the lowest % of species (10.71 %) (Table 3). Estimated number of species shared did not differ greatly from those observed (Table 3).

Several species were identified as indicator species (i.e. with significant indicator values above 70 %) for individual localities, namely *Messor capensis* and *Pheidole* sp.2 for Elandskloofberge, and *Camponotus angustice* for the Malmesbury locality (Table 4). Further, *Messor capensis* and *Messor* sp.1 were indicator species for the Elandskloofberge remnant site, *Monomorium* sp.1 for Malmesbury reserve site and *Linepithema humile* for the Grabouw remnant site (Table 4).

Assemblages structure differed significantly between sites and localities (ANOSIM, Global R = 0.851, p = 0.001 and Global R = 0.611, p = 0.001 respectively). Overall there were thus significant differences in species richness, composition and structure between sites in the region and between localities.

Environmental determinants of ant assemblages
Species richness and abundance

A significant amount of variation in species richness across sites (pooled grid data within sites) as well as grids was explained by soil variables (soilAX1) (Table 5). Ant species richness was negatively related to an increase in an axis that represented mainly decreasing soil resistance and increasing soil moisture, nutrients and % silt component in the soil (Appendix 5D, E & F). Variation in species richness of grids was also significantly explained by sites (Table 5). Ant species richness of individual localities was not significantly explained by any of the PCA axes, except in the Elandskloofberge and Grabouw localities. In the Elandskloofberge locality, climateAX1 and soilAX1 contributed significantly to explaining ant species richness. Hence species richness was positively related to axes representing mainly increasing temperature, increasing soil moisture and increasing soil nutrients (Table 5, Appendix 5G). In the Grabouw locality, soilAX1 and vegetationAX1 were significant in explaining variations in ant species richness. Species richness at this locality was positively related to mainly increasing litter and vegetation height density above 1.5 m, as well as decreasing pH, decreasing soil nutrients and increasing % sand component (Table 5, Appendix 5C).

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Thus overall, sites and soil variables were important in explaining the variation in species richness across sites and grids, with increasing ant species richness being related to decreasing soil nutrient concentrations. Explanatory variables for individual localities varied, with three localities having no significant explanatory variables and the other two having a combination of the climate, vegetation and soil variables.

Ant abundance for sites (pooled grids per site) as well as grids was significantly related to vegetation AX1, so that abundance was negatively related to an increase in vegetation density greater than 0.5 m as well as to mean litter weight and total coarse and fine litter weight (Table 5, Appendix 5A & B). Variation in ant abundance for grids was also significantly explained by sites (Table 5). All ant abundance models for individual localities were significant in explaining ant abundance variation (Table 5). The abundance of ants in the Elandskloofberge locality was negatively related to climate AX1 (i.e. ant abundance was negatively related to mainly an increase in soil temperature). Ant abundance in the Grabouw locality was significantly related to climate AX1 (ant abundance was negatively related to mainly decreasing soil temperature), soil AX1 (ant abundance was negatively related to mainly an increase in sand and a decrease in soil nutrients and moisture) and vegetation AX1 (abundance was negatively related to a decrease in % bare ground and positively to litter weight, % woody component, plant density above 1.5 m, mean litter weight, total coarse and fine litter weight and % fine litter component). In the Stellenbosch locality, abundance was significantly related to soilAX2 (i.e. abundance was positively related to mainly a decreasing % base saturation of Na).

Variations in abundance across sites and grids were significantly explained by sites and vegetation variables, with abundance being negatively related to an increase in vegetation density above 0.5 m and litter content. For individual localities, climate, vegetation and soil were significant explanatory variables for abundance variations, although their role differed for each locality.

None of the spatial terms were significant when using species richness ($p > 0.05$), indicating that no coarse-scale spatial trends were present in ant species richness. For abundance, x and x^2 were significant ($F_{2,47} = 6.63$, $p < 0.01$, $R^2 = 0.19$, x: beta = -234.18, t = -3.60, d.f. = 49, $p < 0.001$, x^2: beta = 235.25, t = 3.60, d.f. = 49, $p < 0.001$). However none of the spatial terms were significant, when adding these terms to the environmental terms in the GLZ ($p > 0.05$). Hence spatial polynomial

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terms were omitted from further analyses and the final models and best fit models were run including only the environmental PCA axes.

Assemblage structure

The first canonical axis in the CCA biplot of ant assemblage and sites (Fig. 6A) explained 11.7 % of the variation in the ant assemblage (F = 5.322, p = 0.002) and the first and second axes together explained 20.05 % of the variation. The first axis broadly separated the Malmesbury sites from the Elandskloofberge sites, while the second axis separated the more northerly sites (with the exception of the Stellenbosch reserve site) from the southerly sites. The second axis site separation coincides with the presence or absence of the Argentine ant, with sites on the right having the Argentine ant present and those on the left without the Argentine ant (Fig. 6A).

For the CCA biplot of ant assemblages and environmental variables (Fig. 6B), the first canonical axis explained 11.1 % of the variation in ant assemblages across the all sites (F = 4.862, p = 0.001) and the first and second axes together explained 18.7 %. Soil nutrients (T-value) (F = 5.01, p = 0.001), % silt component (F = 1.79, p = 0.002), soil moisture (F = 1.52, p = 0.018), soil resistance (F = 2.56, p = 0.001), % base saturation Mg (F = 1.78, p = 0.006) and exchangeable cations Mg (F = 1.56, p = 0.014), % woody component cover (F = 1.50, p = 0.019), foliage height density between 0.25 – 0.50 m (F = 1.75, p = 0.003), plant species richness (F = 3.27, p = 0.001) and mean soil surface temperature (F = 1.66, p = 0.007) added significantly to explaining the variance in ant assemblages. The first axis represents an environmental gradient of increasing soil nutrients, % silt component, soil moisture and exchangeable Mg cation concentration. The second axis represents a decrease in plant species richness and vegetation density between 0.25 – 0.50 m (Fig. 6B). Soil nutrients (T-value), plant species richness and soil resistance together were the most important environmental variable in explaining variance in ant assemblage structure (Fig. 6B).

For the final CCA, where the Argentine ant was removed from the ant assemblage and included as an environmental variables, the first canonical axis explained 10.0 % of the variation in ant assemblages across the all sites (F = 4.201, p = 0.001) and the first and second axes together explained 17.3 %. Presence or absence of the Argentine ant (F = 4.68, p = 0.001), Soil nutrients (T-value) (F = 1.88, p = 0.001), % silt component (F = 1.67, p = 0.007), soil moisture (F = 1.54, p = 0.015),

soil resistance (F = 1.88, p = 0.001), % base saturation Mg (F = 1.40, p = 0.039) and exchangeable cations Mg (F = 1.81, p = 0.004), % woody component cover (F = 1.66, p = 0.006), foliage height density between 0.25 – 0.50 m (F = 1.65, p = 0.005), plant species richness (F = 3.11, p = 0.001) and mean soil surface temperature (F =1.56, p = 0.011) added significantly to explaining the variance in ant assemblages. The first axis represents an environmental gradient of increasing presence of Argentine ant, % silt component, soil moisture, soil nutrients (T-value) and exchangeable Mg cation concentration. The second axis represents an increase in plant species richness, vegetation density between 0.51 - 0.75 m and increasing mean ground temperature (Fig. 6C).

Ant assemblages were therefore separated on the basis of their regions rather than reserve and remnants. Six soil variables as well as two vegetation and one weather variable were significant in separating sites. Excluding the Argentine ant from the ant assemblages and including it as an environmental variable resulted in simply the addition of the presence or absence of the Argentine ant to the previously significant variables.

Beta diversity

More than half of the ant beta diversity was generated at the locality level when using additive partitioning of species richness (Fig. 7, Appendix 7). The $beta_{add}$ (species richness turnover) increased approximately linearly with increasing spatial scale when using three hierarchical levels, namely pitfalls, grids and sites (Appendix 7). Both reserves and remnants had similar partitioning of species richness (Fig. 7, Appendix 7). The $beta_{add}$ between pitfalls in a grid was significantly lower than expected (p < 0.001) by randomly allocating individuals to pitfalls. Species richness turnover between grids in a site and between sites in a locality was higher than expected (p < 0.001) by randomly allocating pitfalls to grids, while keeping them in their sites and randomly allocating grids to sites within their set localities respectively. However the species richness turnover between localities in the region was not significantly higher than expected (p = 0.054). Thus the grid and site within locality as well as sites in the region level were found to be important for generating species richness.

Beta diversity, using $\beta_{sim,}$ (compositional turnover), changed across scales depending on the number of hierarchical levels used. The difference between reserve

and remnant β_{sim} across spatial scale was determined using three levels (between sites in a region, between grids in a site and between pitfalls in a grid). For each of the three levels, β_{sim} was similar for reserve and remnant sites. Additionally across all three levels there was no significant difference in β_{sim} between reserve and remnants (GLM, MS = 0.010, d.f. = 1, p = 0.687) (Fig. 8A). However, compositional turnover was significantly higher between sites in a region than between grids in a site and between pitfalls in a grid (Fig. 8B) (GLM: MS = 0.430, d.f. = 2, p = 0.002). However when including four hierarchical levels (between localities in a region, between sites in a locality, between grids in a site and between pitfalls in a grid), there were no significant differences in β_{sim} across scales (Fig. 8C) (GLM: MS = 0.030, d.f. = 3, p = 0.73). Compositional turnover was highest between localities in a region, when using the four levels, although this was not significant (Fig. 8C). Thus the site within the region level was the most important for generating ant compositional diversity in this study.

DISCUSSION

Ant species richness in the CFR lowlands

The 83 species sampled in this study compares well with the ant species richness values in related studies for the region. For example, a longer term study with greater sample effort conducted across an altitudinal gradient from 0 - 2000 m.a.s.l and down to 500 m.a.s.l. again, across three vegetation types, in the northern Cape Floristic Region, found 85 species (Botes *et al.* 2006). Most other studies on ants conducted in the CFR have covered a much smaller sampling extent and hence trapped considerably fewer species. However, these are comparable to the individual localities that were sampled in this study. For example, 49 species were trapped at the Stellenbosch locality including the Jonkershoek Nature Reserve, while another study conducted in the Jonkershoek Valley captured 45 species in total (Donnelly & Giliomee 1985). Studies conducted in other locations in the CFR included 47 ant species across 14 sites in an area moderately infested with *Acacia saligna* (French & Major 2001) and 27 species captured across three sites along a gradient of *Hakea sericea* infestation in mountain fynbos near George (Koen & Breytenbach 1988). The sampling conducted in this study is thus considered representative of the local species richness of ants. This is strongly supported by the approximate asymptotes to species

richness reached by rarefaction curves (see also Chapter 1). However, the absence of seasonal specialists from a "snap-shot" sample such as this one would have affected sample representivity. Based on the results of the seasonal variation in ant assemblages that was found at one of the sites, i.e. Elandsberg (Chapter 2), about 22 additional species or a 27 % increase in species richness can be expected if sampling is conducted throughout the year, rather than only during spring. Additionally, 75 % of the species that were sampled in spring were not assigned species names, due to a lack of available taxonomic classification, but were left as morphospecies. Systematic changes of ant species may thus still result in either the addition or loss of species to the current total. Nonetheless, because estimated species richness values were very close to those observed, and because richness values obtained were similar to those of previous studies, the richness recorded in this study is considered representative of the spring-active component of the ant fauna in the CFR.

Ant assemblages of reserves and remnants
Species richness and abundance

This study was the first to explicitly examine the differences in ant assemblages between reserve and remnant pairs. In the present study, overall there was no significant difference in ant species richness between reserves and remnants. There were also only small differences in estimated species richness values between reserves and remnants, with a maximum of 5.71 (Jack2) additional species predicted in reserves. Overall, remnants supported 95.7 % of the observed ant species richness that was found in reserve sites. Thus, assuming that ant assemblages are resident in the remnants, overall assemblages in remnants are able to withstand the disturbance levels that have to date been associated with them. Since reserves may themselves be considered as larger remnants of a once continuous landscape, our results could be compared to previous studies investigating species richness changes across remnants of various sizes. Two studies, have shown that ant species richness was similar across remnants of sizes varying from 0.2, 3 and 9 ha (grassland remnants in Sweden (Dauber *et al.* 2006)) and 50, 100 and 300 ha (forest remnants in Brazil (Ribas *et al.* 2005)). These results thus indicate that in other regions of the world, remnants (i.e. small remnants) have been found to support similar ant species richness to that found in reserves (i.e. larger remnants) (Ribas *et al.* 2005, Dauber *et al.* 2006).

Although there were no overall significant differences between reserves and remnants in ant species richness and abundance, there was variation between localities in the differences between reserves and remnants, i.e. two reserve-remnant pairs had significantly lower species richness in remnants, two pairs had no significant difference and one pair had significantly higher species richness in the remnants. Previous studies from across the world have found mixed effects of disturbances on ant species richness (Hoffmann & Andersen 2003, Underwood & Fisher 2006). Generally, significant declines in ant species richness have occurred only in heavily disturbed areas, such as land-use changes from natural to agricultural habitats (Lobry DeBruyn 1993, Gómez *et al.* 2003, Witt & Samways 2004), while disturbances such as grazing and fire have shown both no effects and in some cases positive effects on species richness (Abensperg-Traun *et al.* 1996, Kotze & Samways 1999, Read & Andersen 2000, York 2000, Parr *et al.* 2004). A study in Mexico, for example, found ant species richness to significantly decline from forest fragments to conventionally farmed coffee plantations, however there was no significant decline between fragments and organically grown coffee plantations where many forest tree species remained (Perfecto & Vandermeer 2002). In our study the mixed effects observed in the localities may thus also be due to local differences in levels and intensities of disturbances between localities.

Grading sites according to their disturbance levels is difficult as not only current disturbance, but also historical disturbance regimes play a role (Lunt & Spooner 2005). Based on subjective observations (see study site descriptions), the number of alien plant species present and the presence or absence of the invasive Argentine ant (the effects of this ant are discussed in greater detail later on), Stellenbosch and Grabouw localities showed the greatest differences in disturbance levels between reserve and remnant. Note that although the remnant of the Somerset West locality was probably more disturbed than that of the Stellenbosch and Grabouw locality, the Somerset West reserve condition was considerable poorer than that of either the Stellenbosch or the Grabouw reserve and therefore the difference between reserve and remnants was smaller for this locality than for the other two. Stellenbosch and Grabouw were also those localities where species richness was significantly lower in remnants than in reserves, indicating that the intensity of disturbance may be the reason for observed variation in localities. Reasons for the significantly higher species richness in the remnant of the Elandskloofberge site may be due to the overwhelming

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abundance of the native pugnacious ant, *Anoplolepis steingroeveri*, in the reserve site. This species dominated the grids in the reserve which may have resulted in reduced species richness through the competitive exclusion of other ant species (Andersen 1992). Thus variation between localities in the differences between reserves and remnants may be due to the intensity of disturbance as well as natural ant assemblage patterns. Also, although overall no species richness differences were found between reserve and remnants, higher levels of local disturbance to remnants do appear to result in a significant loss of ant species richness.

Species Composition and Assemblage Structure

Although the general result supports the hypothesis that ants as a taxon are relatively robust to disturbances (Parr *et al.* 2004, Underwood & Fisher 2006), species richness may be too coarse a measure to discriminate overall differences between reserves and remnants, and ant species composition and assemblage structure may be more informative of differences present (Majer & Nichols 1998, Fleishman *et al.* 2005). Disturbances are important in determining the composition and structure of ant communities (Andrew *et al.* 2000, York 2000), with some species increasing in abundance (eurotypic species), while others decrease (stenotypic) (Samways 1981). Functional groups have been shown to respond similarly to disturbances across continents (Andersen 1995), although care should be taken in assigning species to functional groups when scaling down to smaller geographical areas as some species change their functional role within the regional context (Andersen 1997b, Hoffmann & Andersen 2003). Opportunist species (OPP) are known to, in most cases, increase in disturbed habitats and are common in anthropogenic habitats (Bestelmeyer & Wiens 1996, Andersen 1997a, York 2000, Gómez *et al.* 2003, Hoffmann & Andersen 2003). In this study, the OPP species group had the highest species richness of all the functional groups, both overall and in reserves and remnants. One of the OPP species, *Tetramorium quadrispinosum*, was found to be present in every site (reserve and remnant). Although it is an opportunist, this species is an important seed disperser of myrmecochorous plants (Bond & Slingsby 1983) and thus critical for the CFR. The relative number of species per functional group did not differ greatly between reserves and remnants, except for tropical climate specialists (TCS), which were only present in the reserve sites. The two species that contributed to the TCS were *Dorylus helvolus* and *Aenictus rotundatus* (aenictine army ants), both of which occur

throughout Africa (Taylor 2006). However both these species were present in low abundance (5 individuals for both species combined) and therefore TCS differences were not interpreted further. The relative abundance of individual functional groups was substantially different between reserves and remnants, but as mentioned before, these results were biased by the overwhelming abundance of one species, *Anoplolepis steingroeveri* in one grid. Although in other studies functional groups have been found to show marked responses to disturbances (York 2000, Hoffmann & Andersen 2003), here very small differences between reserve and remnant assemblages were found. One reasons for this may be that the functional groups (Andersen 1990, 1995, 1997a) are not sufficiently sensitive or appropriate to detect differences in South African ant fauna. Alternatively, it suggests that in general remnants currently support ant assemblages that are functionally very similar to those of reserves.

Assemblage structure as a measure is generally more sensitive to disturbance than species richness (Majer & Nichols 1998, Fleishman *et al.* 2005). For example, clear differences in ant assemblage structure have been shown between burnt and unburnt plot ant assemblages (York 2000, Parr *et al.* 2004) and grazed and ungrazed plots (Abensperg-Traun *et al.* 1996, Bestelmeyer & Wiens 2001, Woinarski *et al.* 2002, Sobrinho *et al.* 2003). However, in this study, assemblage structures were similar for the overall reserves and remnants, and sites were not clearly separated into reserve and remnants, based on their assemblage structure (CCA). Also only very weak differences were found in ant assemblage structure between pooled reserves and pooled remnants (ANOSIM). Thus overall compositional differences were small between reserve and remnants.

However, similar to the results of species richness, individual localities varied in the structural assemblage differences between reserve and remnant pairs. The localities which had significantly less species in the remnants than in the reserves pair also had significantly different assemblage structures. For the two localities with similar species richness in the reserve and remnant pair, one had similar assemblage structures while the other had significantly different assemblage structures. This emphasises that low species richness differences do not necessarily imply similar ant assemblages. Finally, the locality which had a significantly higher species richness in the reserve than in the remnant, had no significant difference in the assemblage structures, indicating that the reserve and remnant in this locality were similar with many (almost half) shared species. Therefore as was seen with species richness,

overall differences were small between reserve and remnants, however distinct differences were found in some of the localities, indicating that remnants have the potential to conserve ant assemblages similar to those found in reserves, but this potential is not necessarily realized and is likely to be influenced by local disturbance histories.

Ant assemblages between sites and localities

Although overall differences between reserves and remnants were generally weak, ant assemblages differed markedly between localities and across sites, in terms of species richness (observed and estimated), abundance and assemblage structure. Additionally, a significant portion of the variation in species richness was explained by sites. Regional separation of sites by their ant assemblages was thus much stronger than that between reserve and remnant. On average 44 % of species were shared between reserves and remnants, while only 30 % of species were shared on average between localities. Contrasting results have been found in other studies for the relative importance of disturbance and natural underlying spatial variability in a region (Bestelmeyer & Wiens 2001, Woinarski *et al.* 2002). An Australian study concluded land-use to be of greater importance in structuring ant assemblages than differences between sites due to natural spatial variability (Woinarski *et al.* 2002), while in the United States, differences in natural environmental variables were more important in explaining ant richness and compositional variation than changes caused by different grazing intensities (Bestelmeyer & Wiens 2001). Our findings appear to support those of the latter study, where ant assemblages were affected more by natural spatial variability than by disturbances. The CFR is known to be highly heterogeneous, both in terms of its geology and flora (Cowling 1990), and this heterogeneity was mirrored by the ant fauna. Site and locality differences in ant assemblages may therefore be due to natural geological, climatic and floral heterogeneity. However, as mentioned previously, reserves and remnants varied in the intensity of disturbance and therefore some of the variation between sites and localities may also come from variation in disturbance intensities across sites and localities.

Beta diversity

Beta diversity is known to change with spatial scale (Wagner *et al.* 2000, Lennon *et al.* 2001, Koleff & Gaston 2002, Gering *et al.* 2003). Generally studies

using the additive partitioning of species richness of various taxa have found species richness turnover to increase with spatial scale (Wagner *et al.* 2000, Gering *et al.* 2003, Tylianakis *et al.* 2006). This is not surprising, as one would expect that, based on the species-area relationship (Lomolino 2001), as species richness increases with increasing scale, species richness differences between scales would also increase. This study found, species richness turnover (β_{add}) to increase almost linearly with increasing scale, i.e. at three hierarchical scales, from between microhabitats (between pitfalls), to between reserve patches/remnants (between grids) and finally to between reserves/farms in the region (between sites in a region). However, when dividing the highest level (between reserves/farms in the region) into turnover between reserve and farm for each pair (between sites in a locality) and turnover between the reserves with their surrounding farms (between localities), species richness turnover was no longer linear. Turnover between the reserves and remnants was considerably smaller than that between localities. This confirms the overall relatively small species richness difference between reserves and remnants.

In contrast to the linear increase in species richness turnover with increasing scale, the pattern of compositional turnover (β_{sim}) was more complex. Turnover decreased from between pitfalls to between grids and from there increased to between sites and between localities. Compositional turnover in British birds has also been found to both decrease with an increase in spatial scale ($10 - 90$ km^2) (Lennon *et al.* 2001) and to increase with increasing scale ($200 - 1000$ km^2) (Koleff & Gaston 2002). The two bird studies together show an initial decrease at small scales and then an increase at larger scales, a pattern resembling that of our study. Reasons for observing a relatively high compositional turnover between pitfalls, i.e. within a reserve patch/remnant, could be interspecific competition, resulting in a patchy distribution of ant species at this scale (Andersen 1997b, James 2004). The relatively low compositional turnover between reserve patches/remnants indicates that individual ant species generally occurred throughout the reserve/farm. Compositional turnover was highest between reserves/farms in the region as was found for species richness turnover, again emphasizing the importance of the large scale heterogeneity of the region, as has been found in another region (Pfeiffer *et al.* 2003).

The level or spatial scale which is most important for generating diversity differs between taxa and regions (Wagner *et al.* 2000, Gering *et al.* 2003, Chandy *et al.* 2006, Tylianakis *et al.* 2006). Studies using the additive partitioning of species

diversity approach have obtained mixed results, with one study showing greater turnover between plots within a land-use, than between land-uses (Tylianakis *et al.* 2006), while the opposite was seen for vascular plants (Wagner *et al.* 2000). Both these studies however did not investigate whether this turnover was higher than expected and therefore significant. However, a study conducted in the eastern deciduous forest of the USA, found species richness turnover of arboreal beetles between ecoregions was significantly higher than expected and hence factors such as soil type and land-use management were primary in structuring the beetles richness and composition (Gering *et al.* 2003). In our study, the highest, albeit non-significant, species richness turnover occurred between localities in a region. The non-significant results may have been due to the small sample size at this level (n = 5). Typically broad scale heterogeneity of environmental variables would be important in structuring ant assemblages at this level. These variables would also be important for turnover between reserve/farms in the region, which was higher than expected. Environmental variables differed significantly between reserves/farms in the region as well as localities and played a significant role in structuring ant assemblages (see following section). The other levels that were significantly larger than expected were between patches/remnants and between reserves and farms in a locality. Higher species richness turnover between patches/remnants in a site is most probably due to smaller scale variations in environmental variables, while turnover between reserves and farms is likely to be influenced by land-use management and intensity of disturbances (but see following section).

The levels which were most important for generating compositional diversity differed to those generating species richness, with the exception of the between reserve/farms within the region level. The contrasting results of high species richness turnover and low compositional turnover between patches/remnants could be obtained by a high variability in species richness between patches/remnants in a site as well as a high number of shared species between patches/remnants. Thus some patches/remnants may contain only a subset of species that occur in patches/remnants with a higher species richness. This may arise from having a large suite of generalist species which occur throughout the reserve/farm resulting in a low compositional turnover, while one or two individual patches/remnants had a large suite of additional species present, resulting in a high species richness turnover between patches/remnants. These results indicate that not all remnants are equally valuable for

conservation purposes, as some may contain only subsets of species that occur in other remnants on the farm. Contrasting results of compositional and species richness were also found between reserve and remnants in a locality, with significantly high species richness turnover but not significantly higher compositional turnover. This may be due to similar reasons as mentioned above, with many generalist species occurring in reserves and remnants, but with some additional species occurring on either the reserve or remnant. These contrasting results of species richness and compositional turnover for certain levels emphasize the importance of using more than one type of beta diversity measure, as was emphasized by Koleff *et al.* (Koleff *et al.* 2003). Turnover between reserves/farms in the region was however high for both compositional and species richness turnover. Thus this level is essential for generating ant diversity and mirrors the well-known geological and faunal heterogeneity within the CFR (Cowling 1990).

Finally, human-impacts, especially agricultural intensification, has been found to reduce beta diversity, by reducing heterogeneity of the natural landscape (Benton *et al.* 2003). However neither species richness nor compositional turnover had a significantly lower beta diversity for remnants than for reserves at any level in our study. This suggests that for ants remnants in general are no less heterogeneous than the larger reserve areas in the CFR.

Mechanisms underlying ant assemblages including environmental correlates and invasive species

Environmental variables

Many studies have emphasized the effects of changes in vegetation complexity, soil structure and temperature on ant assemblages (Andersen 1986, Lobry DeBruyn 1993, Cerdá *et al.* 1998, Andrew *et al.* 2000, Armbrecht *et al.* 2005, Botes *et al.* 2006). Therefore it is not surprising that soil, vegetation and climate variables in this study significantly explained variation in ant assemblage composition, species richness and abundance.

Soil variables have both direct and indirect effects on ants. Direct effects include the influence of soil texture on ant nest building, while indirect effects occur via the vegetation (Johnson 1992a, Lobry DeBruyn 1993). Ant species differ in their soil preference and are known to nest in soils ranging from hard clay to pure sand (Kaspari 2000). In this study soil variables were important in explaining ant species

richness variation and assemblage composition. The silt component was significant in separating ant assemblages, a result also found in a study conducted in the mountain fynbos of the CFR, about 130 km north this study (Botes *et al.* 2006). This may be a reflection of differences in soil texture preference for nesting in ant species (Kaspari 2000). The mountain fynbos study found ant species richness to be negatively related to phosphorous concentration and positively to pH and that carbon content, clay and silt components and pH were significant in separating ant assemblages (Botes *et al.* 2006). Although the present study did not identify these specific soil variables, a general trend of increasing nutrients (amongst them P) and pH was also related to a decrease in ant species richness. The exact reason for declining species richness with increasing soil nutrients is unclear, but is probably related to the relationship between vegetation and soil variables.

Vegetation variables are known to play a large role in shaping ant assemblages, not only by altering food availability and resources, but also by changing microclimatic conditions for ants (Bestelmeyer & Wiens 1996, Samways *et al.* 1996, Beattie & Hughes 2002). Vegetation variables explained a significant portion of the variation in ant abundance and were significant in separating ant assemblage structure in this study. In the mountain fynbos study, % vegetation cover and vegetation age since last fire, were important in structuring ant assemblages, while % bare ground was significant in explaining species richness (Botes *et al.* 2006). Further, % litter, % vegetation cover, vegetation density and vegetation age since last fire were significant in explaining ant abundance variations (Botes *et al.* 2006). Similar vegetation variables were found to be important in this study. However the measures used in this study were separated into individual constituents, for example % vegetation cover was separated into % grass, % herbaceous component and % woody. Litter was one of the vegetation variables that contributed significantly to explaining ant abundance in this study. Several studies have shown a negative relationship between ant abundance and litter cover (Bestelmeyer & Wiens 1996, York 2000), as was observed in this study. Since litter reduces the efficiency of epigaeic ants in finding, retrieving and safeguarding resources (Andersen 2000), abundance is expected to decline. An increase in litter may also reduce the trapping efficiency of ants using pitfall traps and hence may have reduced trapped ant abundances (Bestelmeyer *et al.* 2000, York 2000). This may explain the significant negative relationship of ant abundance with litter. However the mountain fynbos study showed the opposite trend (Botes *et al.*

2006). Reasons for this are not clear. Not only litter, but also vegetation density was important in structuring ant assemblages, with ant abundance being negatively related to vegetation density above 0.5 m. A possible reason is that an increase in foliage density above 0.5 m could increase the shade in the grid, thereby reducing ground temperatures and so reduce forager abundances (Retana & Cerdá 2000, Lassau & Hochuli 2004).

Ants are a known thermophilic taxon (Hölldobler & Wilson 1990), increasing with increasing temperature, although most are not able to withstand extreme hot and dry conditions (Kaspari 2000). Low temperatures are thought to be primary in structuring ant assemblages globally (Andersen 2000) and were also important in structuring ant assemblages across an altitudinal gradient in the CFR (Botes *et al.* 2006). In this study, overall species richness and abundance variation was not significantly explained by weather variables, including temperature. However ant assemblages were structured by mean ground temperature and in two localities weather variables were significant explanatory variables for species richness and/or abundance.

Environmental explanatory variables differed within localities, but played an important role in explaining variation between localities in differences between reserve and remnant ant assemblages. For example, ant assemblages (species richness and assemblage structure) differed significantly between reserve and remnant pairs for Grabouw and Stellenbosch localities. These localities however also had significant differences in soil variables (both localities) and vegetation variables (Stellenbosch only), which were significant in explaining the variation in ant species richness and /or abundance and in separating ant assemblages in the two localities. In contrast, in localities for which ant assemblages of reserve and remnant pairs were similar, Somerset West and Malmesbury, there were no significant differences in environmental variables and no individual environmental variables significantly explained variations in ant species richness and abundance. Whether the significant differences in environmental variables between reserve and remnant in some localities are due to natural heterogeneity in the landscape or rather as an effect of disturbances on the remnants is not entirely clear. Disturbances are known to alter soil, vegetation and microhabitat variables (Saunders *et al.* 1991), however as mentioned earlier, the CFR is also a highly heterogeneous environment (Goldblatt & Manning 2002) and the greater distance between reserve and remnants in the Stellenbosch and Grabouw

localities, compared to the other locality pairs, may also have contribute to significantly different environmental factors.

This study supports the general findings of the importance of environmental variables in structuring ant assemblages. The large significance of soil variables, especially soil nutrients, and smaller roles of vegetation and temperature were particularly clear.

Invasive species

The Argentine ant, a globally important invasive species, has invaded most of the world's Mediterranean ecosystems, among them the CFR (Suarez *et al.* 1998, Addison & Samways 2000, Walters 2006). In this study, the Argentine ant was present in the southern localities, but absent from the northern localities (Malmesbury and Elandskloofberge). The species is known to prefer moister, cooler areas (15 -19 °C) (Witt & Giliomee 1999, Holway 2005, Thomas & Holway 2005). Since Malmesbury and Elandskloofberge have a lower rainfall and warmer temperatures (Malmesbury locality had significantly higher temperatures compared to the other localities) this may limit the distribution ability of the Argentine ant in these regions (Addison & Samways 2000, Menke & Holway 2006).

The Argentine ant is globally notorious for displacing native ant species (Holway 1998, Suarez *et al.* 1998, Christian 2001). In this study, sites were clearly separated on the basis of the presence or absence of the Argentine ant and species richness was significantly lower where the species occurred compared to sites where it was absent. *Tetramorium quadrispinosum* is known to be able to co-occur with the Argentine ant, while *Anoplolepis custodiens* is thought to be negatively affected by the presence of the Argentine ant (Witt & Giliomee 1999, Addison & Samways 2000). In this study, *A. custodiens* was found only in sites where the Argentine ant was absent, possibly indicating that there is competitive exclusion by the Argentine ant, while *T. quadrispinosum* occurred in every site (both with Argentine ant absent and present), indicating its tolerance to the presence of the Argentine ant.

A study conducted in southern California, found that the Argentine ant had invaded fragments completely, while only the edges of larger unfragmented areas were invaded (Suarez *et al.* 1998). Based on the Californian study, reserves could be expected to be largely uninvaded, while remnants are severely invaded. In this study, occupancy of the Argentine ant was higher in remnants than reserves in all localities

were it was found. Also, the Argentine ant was a characteristic species of remnant sites, indicating that indeed remnants in the CFR are likely to be more susceptible to the invasion of this species.

The presence or absence of the Argentine ant may also explain the differences or lack of differences observed between reserve and remnants of individual localities, as mentioned previously. The Grabouw locality had a higher abundance and occupancy of the Argentine ant in remnants than reserves, which may explain the significantly lower species richness in reserves to remnants and also the significant differences in assemblage structure between reserve and remnant. In contrast the Somerset West locality had an equally high relative abundance of the Argentine ant in reserves and remnants and hence no significant difference is observed between ant species richness and assemblage structure. Thus the Argentine ant has a distinct negative impact on ant assemblages of the CFR and reduces the ability of remnants to conserve ant species diversity.

Conclusion

Overall ant assemblages were similar for reserve and remnants, in terms of species richness, assemblage structure and beta diversity and thus remnants can be considered to contribute highly to the conservation of ant assemblages in the CFR lowlands. This is encouraging for conservation strategies in this biodiversity hotspot, especially since studies of other taxa in the CFR have shown similar results. Even small remnants (< 1 ha or ± 4 ha) were shown to be able to support vegetation that is very similar to that of larger remnants (> 30 ha), provided fire regimes are maintained in the smaller remnants (Bond *et al.* 1988, Cowling & Bond 1991, Kemper *et al.* 1999). A study of insect pollinators on fragments of renosterveld between agricultural fields in the CFR lowlands, showed no significant differences in species richness between fragments of > 30 ha, 3 -10 ha and 0.5 - 2 ha (Donaldson *et al.* 2003). Ants are important seed dispersers in the CFR and therefore their persistence in human-influenced areas also has important implications for plant genera such as *Leucospermum*, *Leucodendron* and *Mimetes*, and their long-term survival (Beattie & Hughes 2002).

However, individual localities show that the potential that these remnants have to conserve biodiversity is diminished considerably by increasing levels of disturbance, such as invasion by the Argentine ant and increasing soil nutrients by

fertilization. Although the negative effects of the Argentine ant on native ant assemblages are known from other regions, the mechanism by which increased soil nutrients affects ant assemblages is not clear. This implies that careful management of remnants is important in order to realize the potential of these areas for conservation. Additionally, the beta diversity results suggest that not all remnants on a farm have equal value for conservation. Thus care should be taken in selecting remnants for conservation attention.

There are however two possible reasons for small differences found between reserves and remnants. The first is that remnants are in fact able to conserve ant assemblages. Alternatively the reserves, themselves only larger remnants, may have already lost many specialist species and only generalist species remain (Samways 1990, Tscharntke *et al.* 2002, Woinarski *et al.* 2002, Major *et al.* 2003). Although for example the Hottentotsholland and Stellenbosch reserves are large including mountain ranges, others like the reserve of the Somerset West locality is relatively small and surrounded by urban development and the reserve of the Malmesbury locality is surrounded by alien vegetation. Comparing current species list with historical ones is difficult, as there are only very few historical records of ant species in the CFR and identification to morphospecies only, does not allow for accurate comparisons. The only study which sampled in an area similar to one of the sites sampled here, used Dietrick's Vacuum sampling and sampled throughout the year (Schlettwein & Giliomee 1987), which makes a once off comparison difficult. Reserve sites did however appear to be dominated by species that were also able to persist in remnants and disturbed areas, indicating that perhaps specialist species have already been lost (Gaston *et al.* 2001, Rodrigues & Gaston 2001, Deguise & Kerr 2006). Nonetheless, although it is not possible to say with certainty whether sensitive species have already been lost, this study does indicate that remnants currently contribute highly to the conservation of ant assemblages that are present in reserves today.

In conclusion, overall ant assemblages of the CFR lowlands were similar between reserves and remnants. Ant assemblages showed greater differences between localities than between reserve and remnants, with soil variables, such as concentration of nutrients as well as amount of litter being primary in structuring ant assemblages. Also, diversity of ant assemblages was mainly generated between sites in the region, rather than between reserves and remnants in a locality. The relatively

high heterogeneity of ants found in this study emphasizes the conservation significance of invertebrates along with that of plants in the CFR. Although some remnants clearly show the potential to conserve ant assemblages, these areas need to be managed correctly so as to maximize the potential. Disturbances such as the presence of the invasive Argentine ant and increasing soil nutrients by fertilizing, pose a distinct threat to the ability of remnants to conserve ant assemblages. Although it is not clear whether remnants are able to support ant assemblages that were once present of the broader CFR, this study showed that some remnants of natural habitat in human-influenced areas currently support ant assemblages representative of those in the CFR today. Therefore currently some remnants do contribute highly to the conservation of a functionally important taxon in this global biodiversity hotspot and if remnants can be managed correctly, may continue to do so in the future.

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Table 1 Species richness estimates ± standard deviation of estimators (Jack 2, Jack 1, ICE and Chao2), as calculated by Estimate S (with replacement), across the various hierarchical levels. Different letters for paired sites indicate significant differences at the 0.05 level.

Hierarchical level	S(obs)	Jack 2	Jack1	ICE	Chao2
Region	83	84.59 ±9.34	86.15 ± 4.38	83.31 ± 4.96	83.16 ± 2.67
Reserve	69	71.82 ± 9.91 **a**	72.7 ± 4.84	70.38 ± 5.1	69.98± 2.91
Remnants	66	66.11 ± 9.38 **a**	69.36 ± 4.12	67.65 ± 4.57	66.46 ± 2.21
Localities					
Elandskloofberge (EB)	42	43.99 ± 8.56	44.85 ± 3.96	44.23 ± 5.15	43.8 ± 3.04
Malmesbury (MB)	38	39.64 ± 6.5	40.1 ± 3.22	39.21 ± 3.75	38.7 ± 2.45
Grabouw (GW)	43	45.52 ±10.06	46.31 ± 4.49	45.7 ± 6.24	45.88 ± 3.71
Stellenbosch (STB)	49	51.56 ± 8.9	52.51 ± 4.19	51.25 ± 4.91	50.88 ± 3.16
Somerset West (SW)	24	24.98 ± 4.71	25.09 ± 1.97	24.39 ± 2.57	24.68 ± 2.04
Sites					
EB reserve	26	28.15 ± 8.12 **a**	27.91 ± 3.76	29.36 ± 11.14	30.71 ± 5.03
EB remnant	36	38.19 ± 7.52 **b**	38.52 ± 3.56	38.06 ± 5.13	39.83 ± 4.09
MB reserve	30	31.93 ± 6.88 **a**	31.67 ± 3.26	31.28 ± 4.76	32.61 ± 3.89
MB remnant	29	31.43 ± 8.18 **a**	30.99 ± 3.91	31.86 ± 7.49	33.73 ± 5.03
GW reserve	34	35.26 ± 7.27 **a**	36.01 ± 2.82	35.54 ± 4.57	37.13 ± 3.5
GW remnant	21	22.38 ± 7.1 **b**	22.7 ± 2.49	23.67 ± 6.73	24.25 ± 3.57
STB reserve	34	35.81 ± 7.55 **a**	36.25 ± 3.46	35.89 ± 5.37	38.19 ± 4.4
STB remnant	25	26.61 ± 5.64 **b**	26.79 ± 2.32	26.6 ± 3.90	27.32 ± 3.04
SW reserve	22	23.1 ± 5.73 **a**	23.23 ± 2.15	23.21 ± 4.01	24.07 ± 2.87
SW remnant	18	18.71 ± 3.83 **a**	18.67 ± 1.74	18.29 ± 2.68	18.23 ± 1.77

Table 2 Shared species richness, observed, % observed of total and estimates (using SPADE) for paired reserve and remnant sites in five localities across the Western Cape Province.

Locality	% Shared (observed)	Observed shared	Estimated shared
Elandskloofberge	47.62	20	26.53
Malmesbury	55.3	21	21.66
Grabouw	27.91	12	12.00
Stellenbosch	20.41	10	10.67
Somerset West	66.67	16	23.02

Table 3 Number of species shared between five localities across the Western Cape Province, showing observed (lower left) (% of total given in brackets) and estimated (upper right) (using SPADE (Chao & Shen (2003-2005))) values.

	Elandskloof-berge	Malmesbury	Grabouw	Stellenbosch	Somerset West
Elandskloofberge		*23.65*	*27.64*	*29.18*	*23.65*
Malmesbury	20 (33.33)		*25.43*	*25.50*	*6.00*
Grabouw	24 (39.34)	19 (30.65)		*31.91*	*23.13*
Stellenbosch	27 (42.19)	22 (33.85)	30 (48.39)		*19.58*
Somerset West	20 (24.53)	6 (10.71)	21 (45.65)	19 (35.19)	

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Table 4 Significant Indicator Values for pooled reserves and pooled remnants, localities and sites. Species for each site and locality are in descending order of Indicator Values. Only Indicator Values above 50% are shown.

Hierarchical Level	Species	% IndVal
Regional		
Remnant sites combined	*Linepithema humile*	54.83
Reserve sites combined	none	
LOCALITIES		
Elandskloofberge locality	*Messor capensis*	79.15*
	Pheidole sp.2	70.99*
	Crematogaster sp.1	64.44
	Anoplolepis steingroeveri	58.80
	Tetramorium sp.1	50.00
Malmesbury locality	*Camponotus angustice*	90.00*
	Ocymyrmex sp. 2	63.74
	Camponotus niveosetosus	60.00
	Lepisiota sp. 2	55.81
Grabouw locality	*Tetramorium* sp. 9	64.51
	Linepithema humile	50.19
Stellenbosch locality	none	
Somerset West locality	*Tetramorium* sp. 3	61.63
	Tetramorium sp.12	53.33
SITES		
Elandskloofberge remnant site	*Messor* sp.1	80.00*
	Messor capensis	77.69*
	Tetramorium sp.1	54.63
	Pheidole sp.2	54.58
Malmesbury reserve site	*Monomorium* sp.1	75.86*
	Monomorium sp.3	60.00
	Anoplolepis custodiens	59.09
Malmesbury remnant site	*Camponotus angustice*	59.62
	Ocymyrmex sp.2	51.77
Grabouw remnant site	*Linepithema humile*	83.29*
	Tetramorium sp.9	52.10
Stellenbosch reserve site	*Tapinoma* sp.2	60.00
	Camponotus sp.11	58.18
	Solenopsis sp.2	55.47
Stellenbosch remnant site	*Meranoplus peringueyi*	66.27
	Tapinoma sp.3	60.00

*Indicator Values above 70 % (subjective benchmark for indicator species (van Rensburg *et al.* 1999, McGeoch *et al.* 2002).

Table 5 Generalized Linear Model (Poisson error distribution, log-link function, Type III results) results for relationship between species richness and abundance of ant assemblages with environmental variables (PCA axes). Abundance models were corrected for over dispersion. Estimates are given in brackets and significant axes are bold. Two separate models were run for grids one with environmental variables and the other with sites as a categorical factor.

Model	Hierarchical level	d.f.	Dev	Selected environmental terms	χ^2	p	% deviance explained
	Species richness						
1	Sites (pooled grids)	6	3.24	climAX1 (-0.11) **soil AX1***(-0.24) veg AX1 (0.01)	9.22	0.03	74.0
2	Grids	46	59.96	climAX1 (-0.04) **soilAX1***(0.11) vegAX1 (0.01)	10.87	0.012	15.3
3	Grids	40	40.79	**sites****			42.4
	Localities						
4	Elandskloof-berge	6	13.00	**climAX1***(0.37) **soil AX1**** (0.26) veg AX1 (-0.22)	8.48	0.04	40.0
5	Malmesbury	6	4.42	climAX1 (0.09) soil AX1 (0.10) veg AX1 (-0.01)	2.10	0.55	
6	Grabouw	6	2.05	climAX1 (-0.08) **soilAX1*** (0.29) **vegAX1***(0.27)	18.84	<0.001	90.2
7	Stellenbosch	5	2.16	climAX1 (-0.03) soilAX1 (-0.12) vegAX1 (-0.12)	1.70	0.64	
8	Somerset West	6	2.39	climAX1 (-0.29) soilAX1 (-0.20) vegAX1 (0.14)	3.91	0.27	
	Abundance						
9	Sites (pooled grids)	6	2949.59	climAX1 (-0.14) soil AX1 (0.03) **veg AX1*** (-0.71)	5378.26	<0.001	64.58

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Model	Hierarchical level	d.f.	Dev	Selected environmental terms	χ^2	p	% deviance explained
10	Grids	45	15001.3	clim AX1(0.22) soil AX1 (0.10) **veg AX1*** (-0.58)	4454.14	<0.001	20.00
11	Grids	40	12137.1	**sites****			41.2
	Localities						
12	Elandskloof-berge	6	5139.1	**climAX1***(-1.95) soil AX1 (-0.63) veg AX1 (1.13)	6798.18	<0.001	60.0
13	Malmesbury	6	88.7	climAX1 (-0.12) soil AX1 (-0.17) veg AX1 (0.05)	77.19	<0.001	46.5
14	Grabouw	6	97.1	**climAX1***(-0.29) **soilAX1****(-0.49) **vegAX1****(-0.31)	169.1	<0.001	91.1
15	Stellenbosch	5	74.58	climAX1 (0.15) soilAX1 (0.02) **soilAX2**** (0.45) vegAX1 (-0.19)	228.74	<0.001	75.41
16	Somerset West	6	93.6	climAX1 (-0.23) soilAX1 (0.18) vegAX1 (-0.35)	177.76	<0.001	65.50

* P < 0.05, ** P < 0.01

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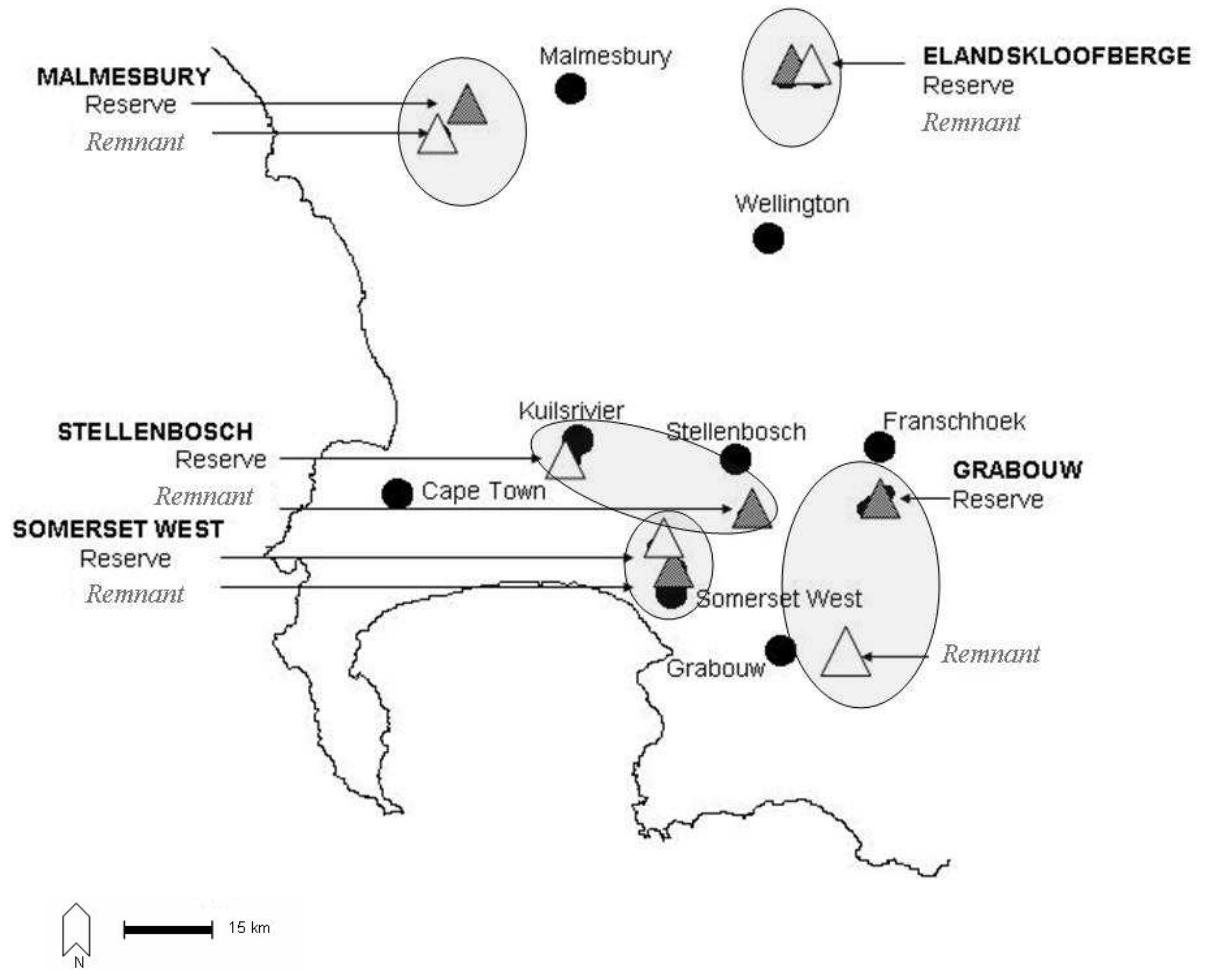
Figure 1 Map of study sites in the Western Cape, South Africa. Shaded areas indicate localities, open triangles indicate remnant sites and filled triangles represent reserve sites.
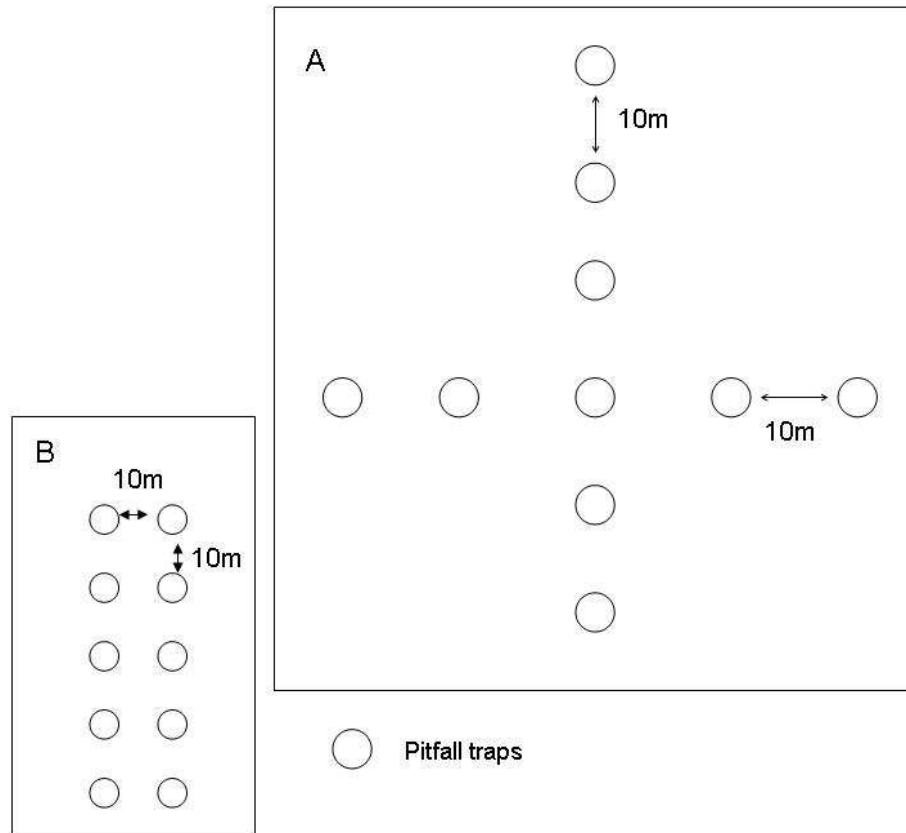
Figure 2 A Pitfall cross array used in all grids except for those in Elandskloofberge sites, where a (2 x 5) grid was used **B**.

A

B
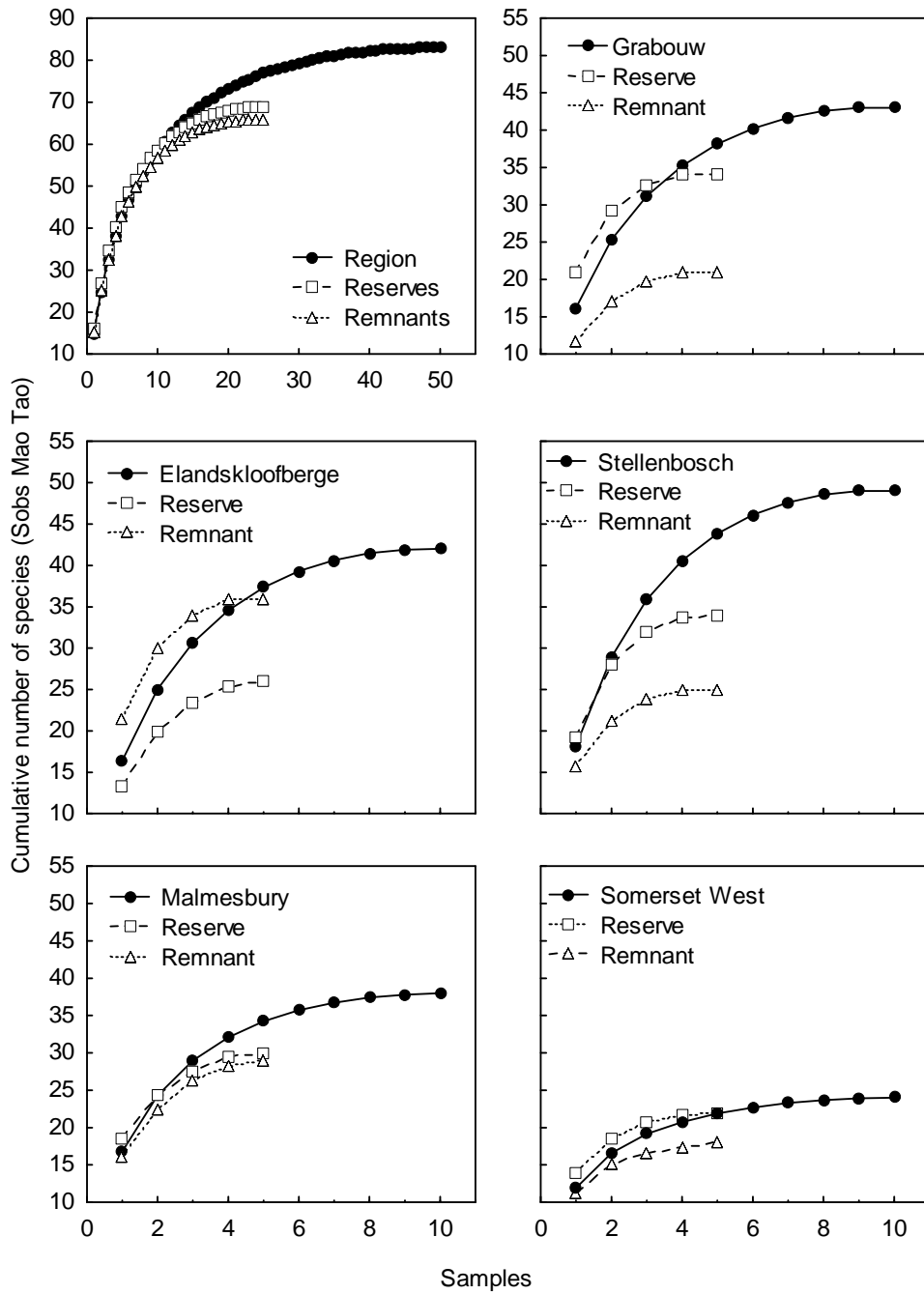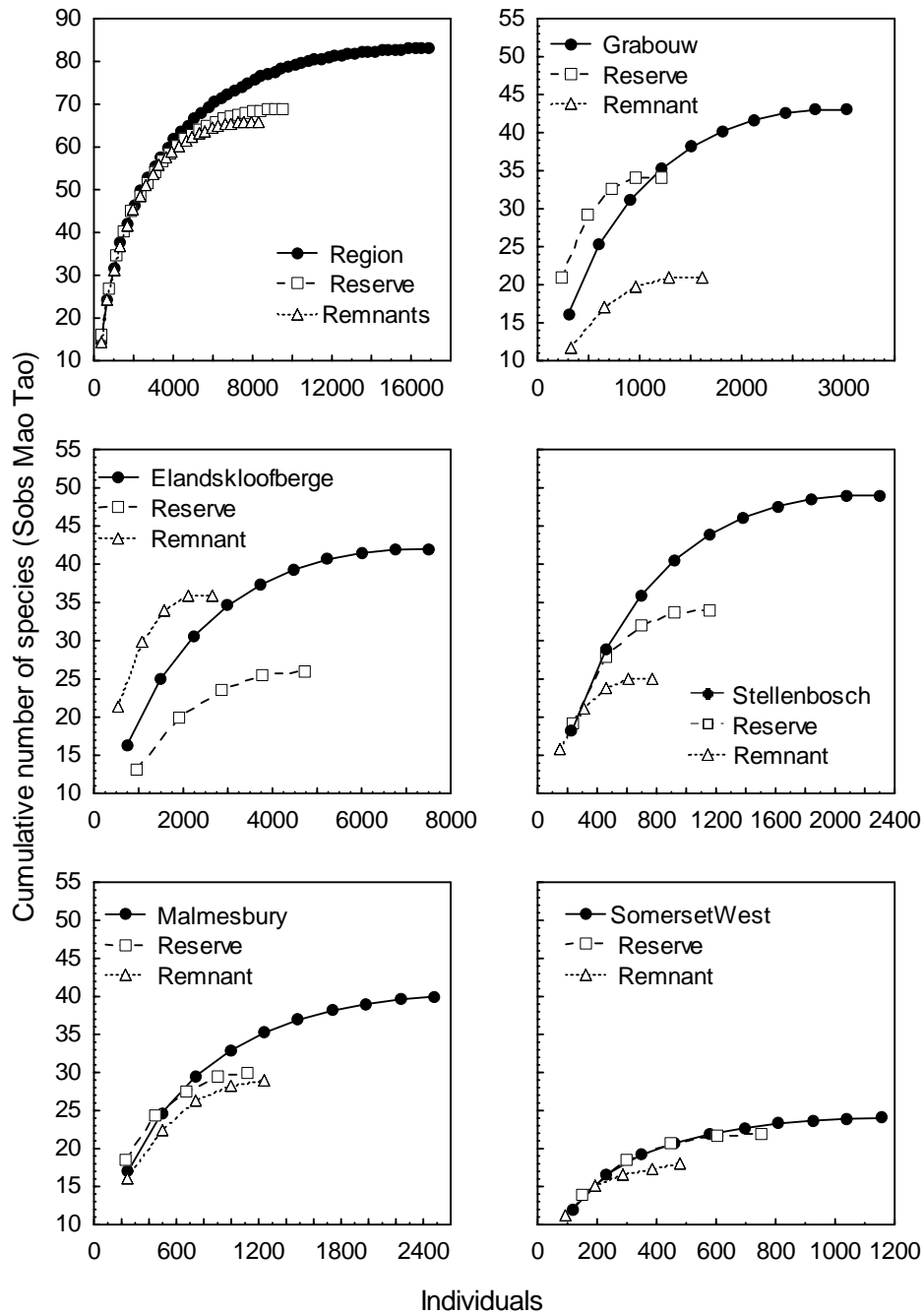
Figure 3 Sample-based rarefaction curves **A** of species and samples and **B** species and individuals using EstimateS calculated Sobs (Mao Tao), sampling without replacement, for the region, localities, and the corresponding paired reserve and remnant sites.

A

Rank abundance (%)

Ant species

Malmesbury

Elandskloofberge

Region

Somerset West

Stellenbosch

Grabouw
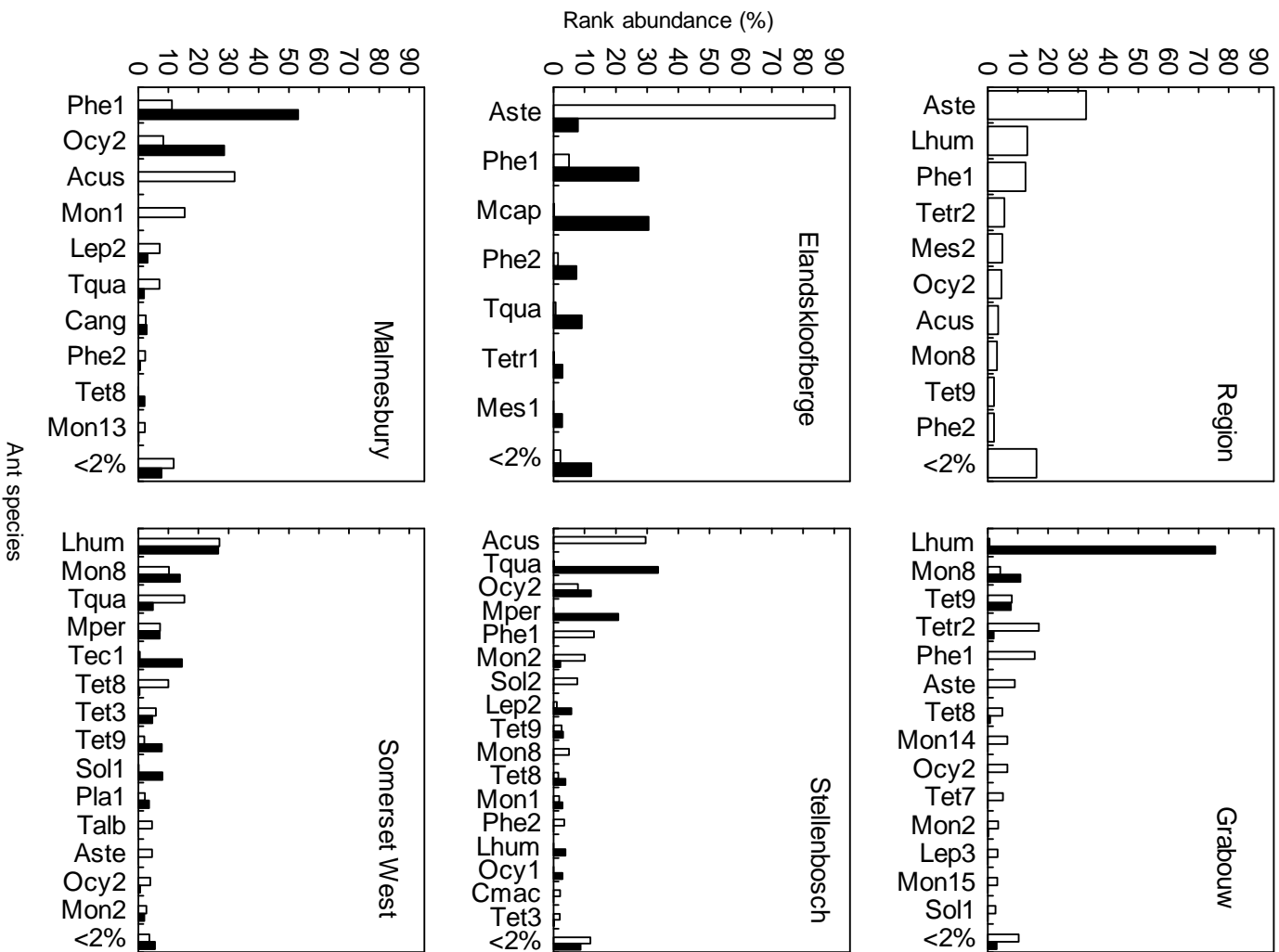
B
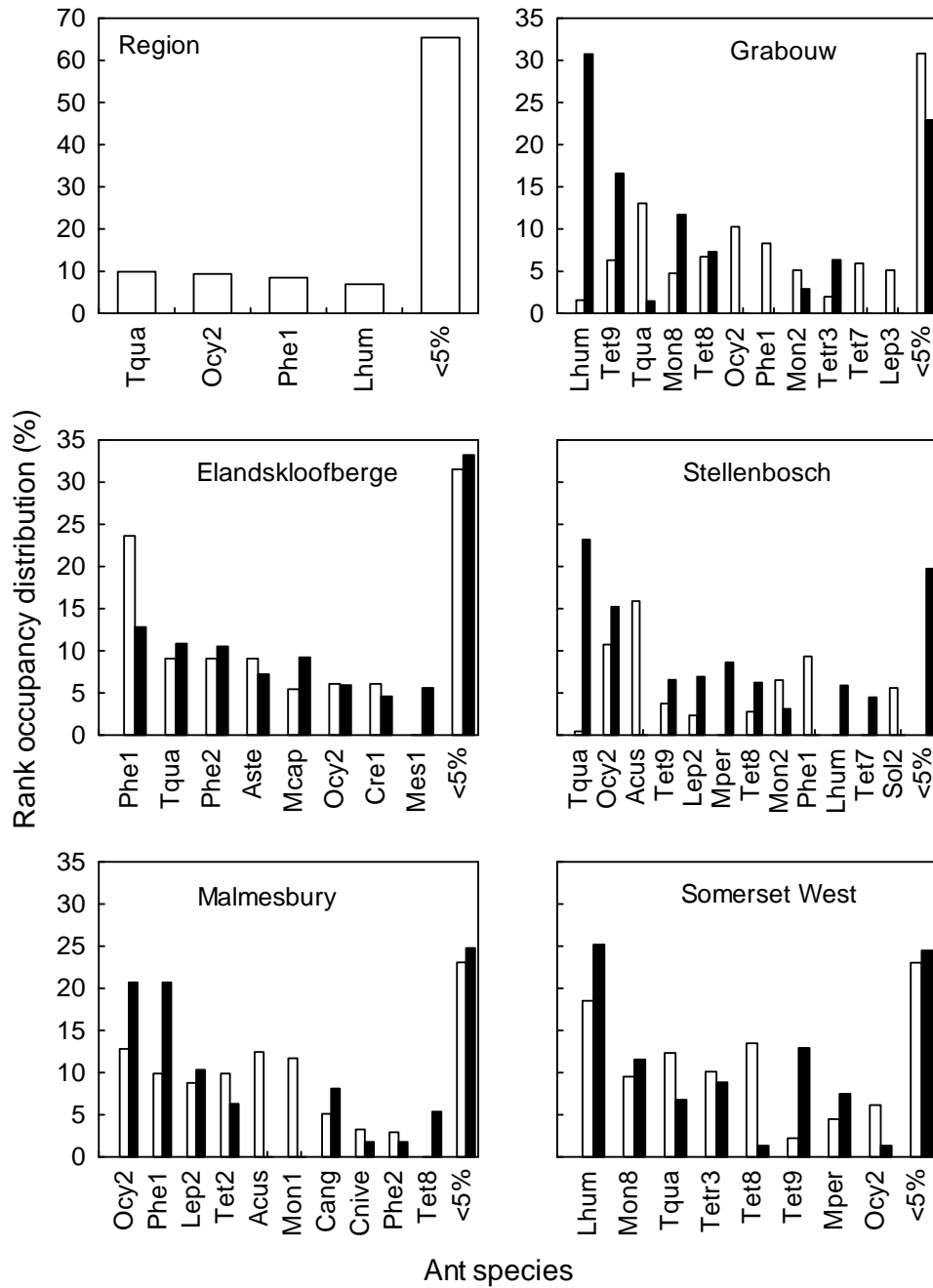
Figure 4A Rank abundance and **B** rank occupancy distribution of ants for the overall region, and reserve-remnant pairs for each of the five localities. Open bars = nature reserve and filled bars = remnant sites. See Appendix 6 for ant species abbreviations. Species which had a relative abundance of less than 2 % and occupancy less than 5 % for the area were summed together in the last bar (< 2 % and < 5 % respectively).

A
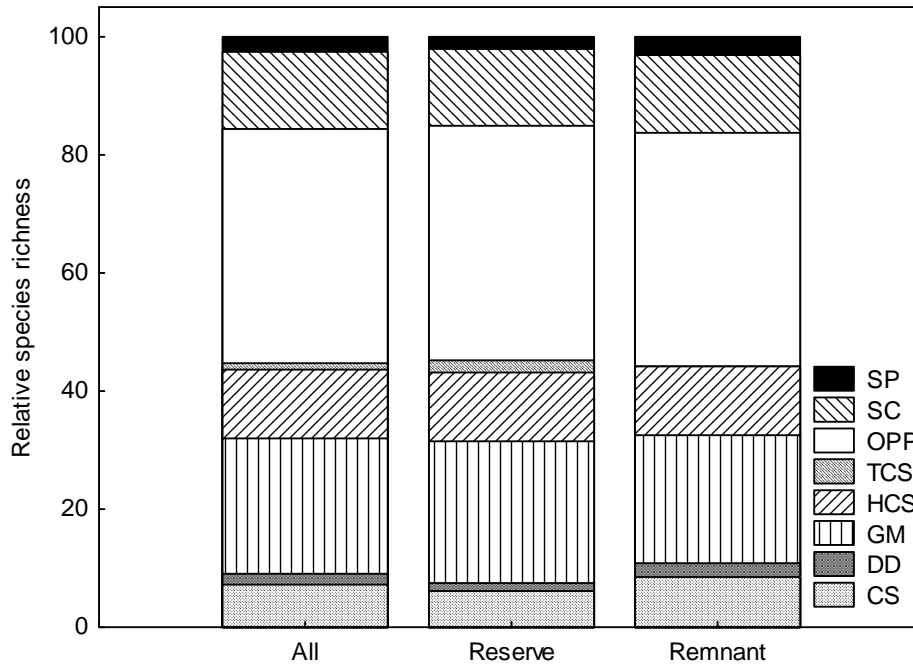
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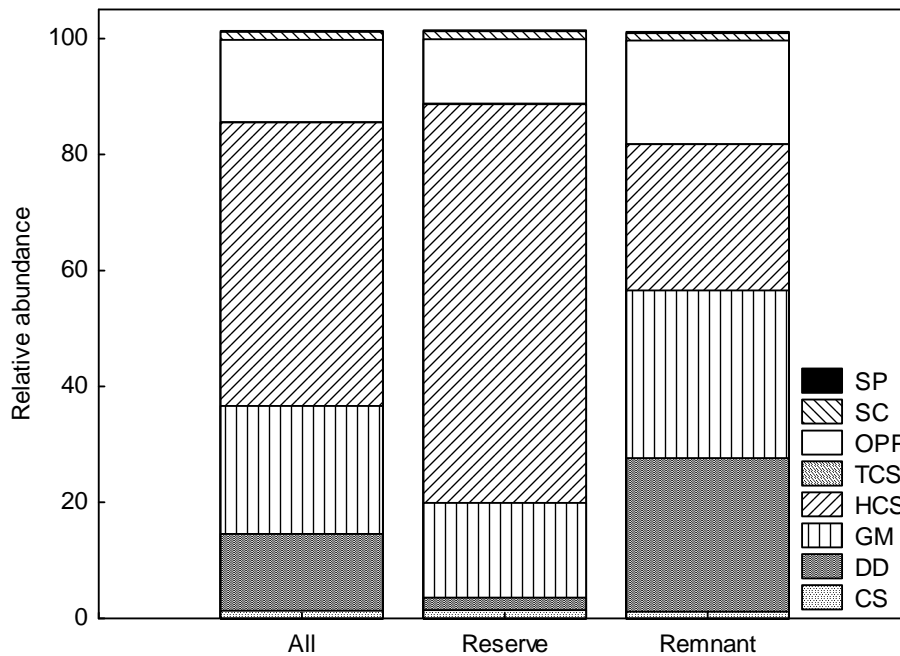
Figure 5 Ant functional groups using **A** species richness data and **B** abundance data for all sites and for reserve and remnant sites separately. SP = Specialist Predators, SC = Subordinate Camponotini, OPP = Opportunists, TCS = Tropical Climate Specialist, HCS = Hot Climate Specialist, GM = Generalized Myrmicinae, DD = Dominant Dolichoderinae, CS = Cryptic Species.

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A

B

C
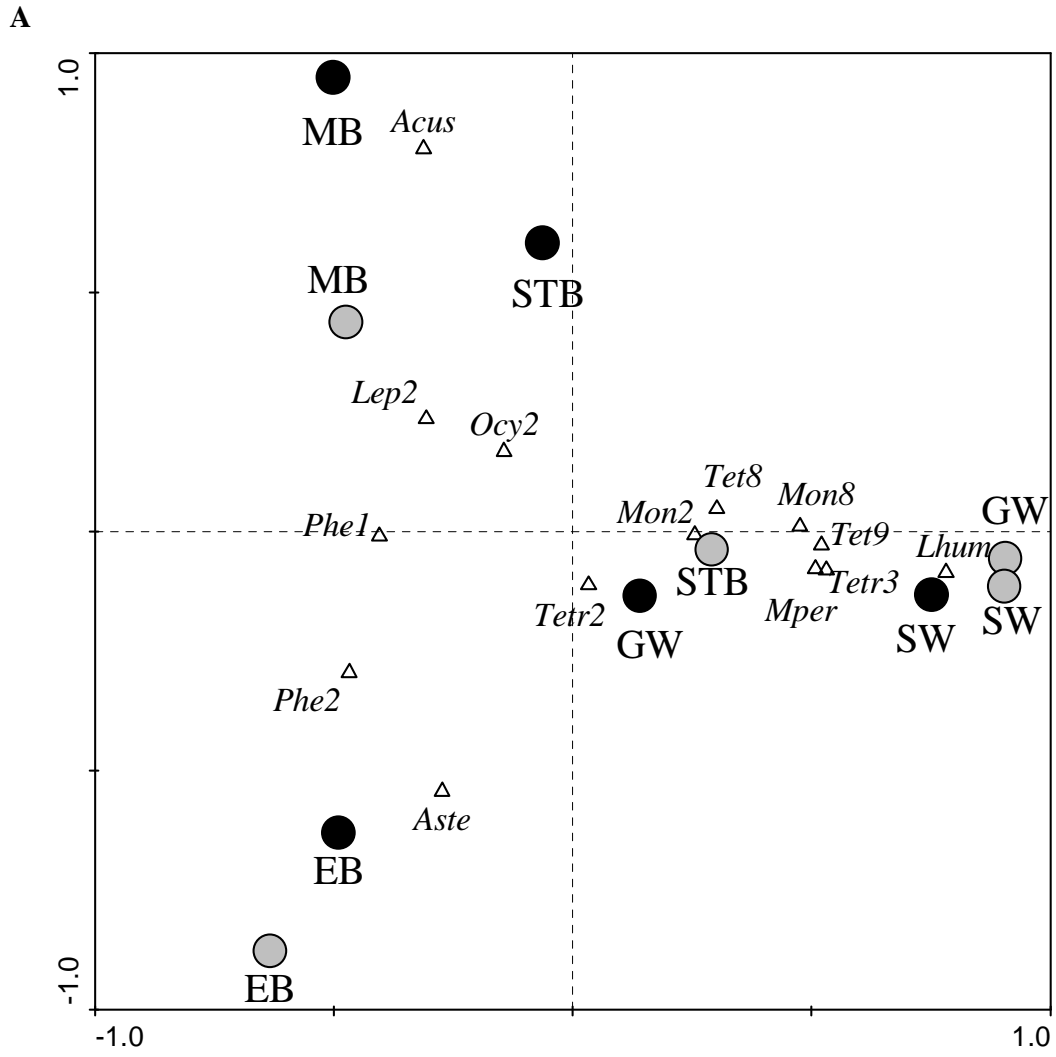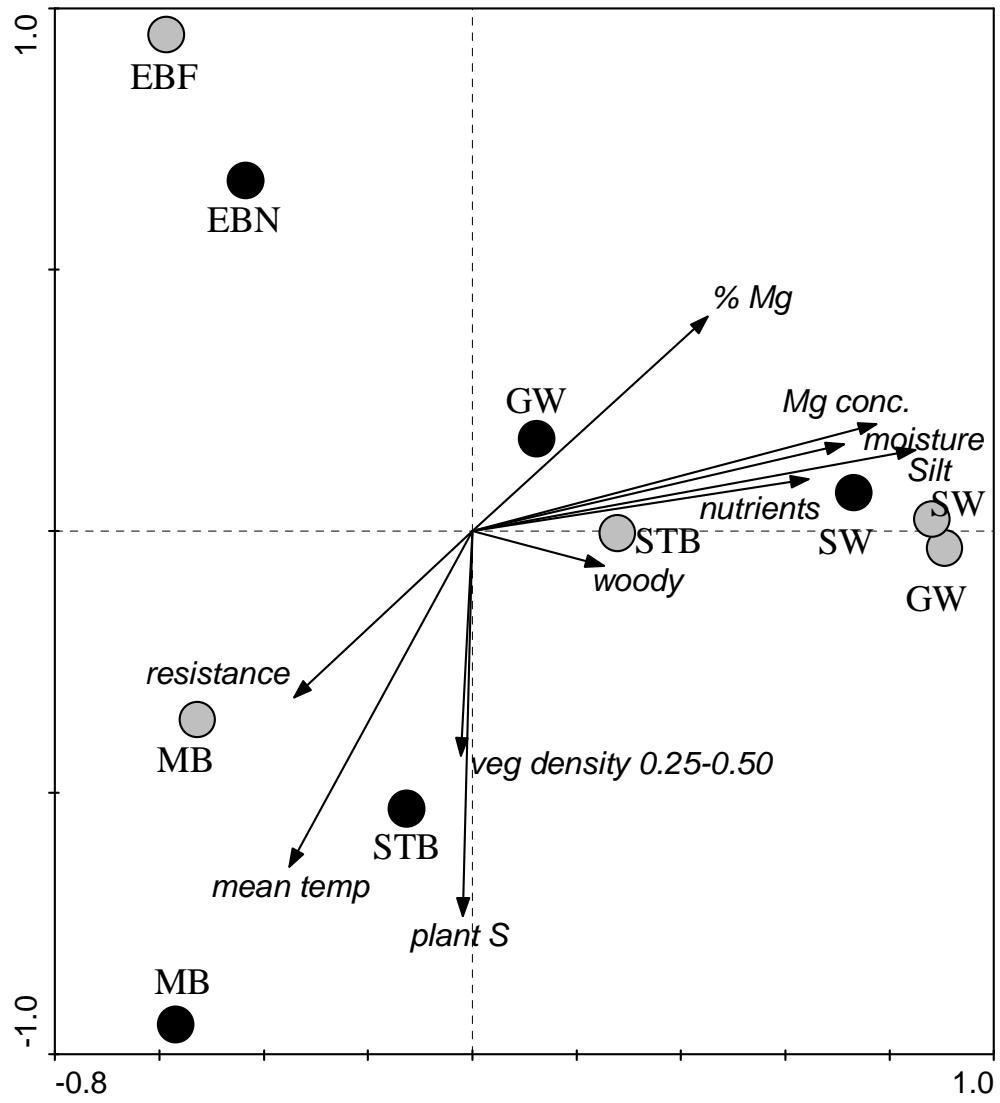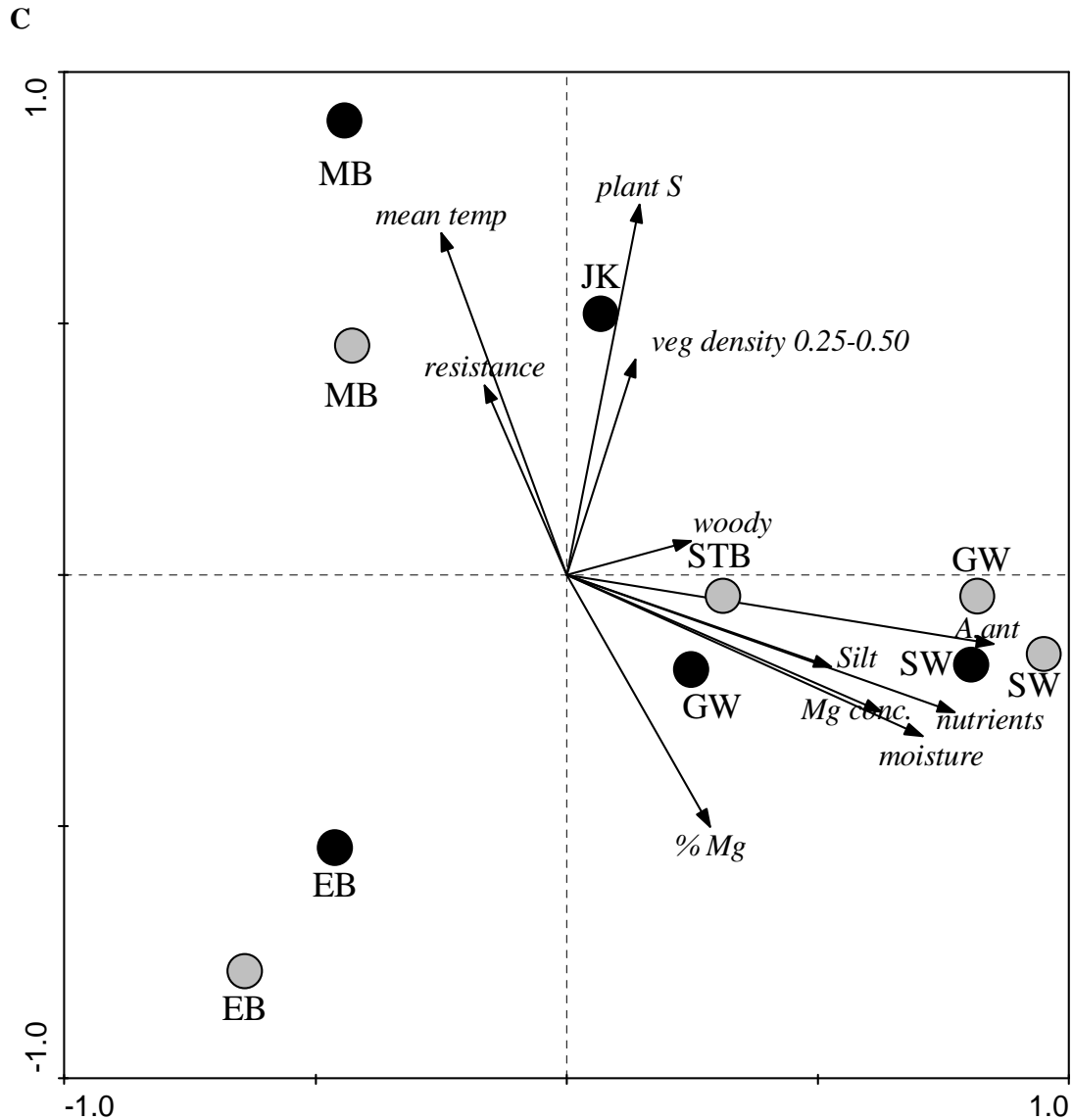
Figure 6 Canonical Correspondence Analysis (CCA) biplots of **A)** ant species and sites, **B)** environmental variables (sites are for illustrative purposes) and **C)** same as B, except excluding Argentine ant for species matrix and adding it as an environmental variable. Only ant species (Appendix 6) which had more than 30 % of their variability explained by the ordination subspace were shown in Fig 6B. Significant environmental variables for **B)** are soil **nutrients** (T-value), % **silt** component, **%** base saturation **Mg**, Exchangeable Mg cations (**Mg conc**.), % soil **moisture,** soil **resistance**, **% woody** plant cover, **veg**etation **density** (0.25 - 0.50 m), plant species richness (**plant S**) and mean ground temperature **(mean temp)**. For **C)** same variables as for B) and Argentine ant presence/absence (**A.ant**). Locality names: EB = Elandskloofberge, MB = Malmesbury, GW = Grabouw, STB = Stellenbosch, SW = Somerset West. Reserve sites of localities are indicated in black and remnant sites in grey circles.
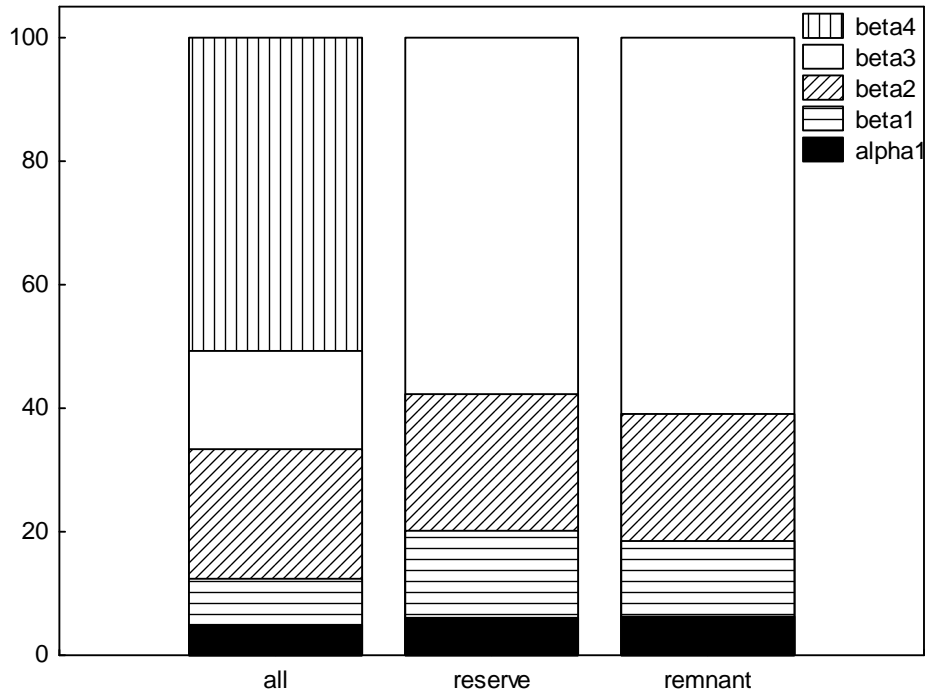
Figure 7 Additive partitioning of species richness. Percentage of total species richness explained by alpha and beta components of diversity at four sampling scales: within pitfalls (alpha 1), between pitfalls (beta1), between grids (beta 2), between sites (beta 3) and between localities (beta 4) for all data combined, reserves and remnants. Since there were reserve and remnant sites in each locality, no locality data is given.

A

B

C
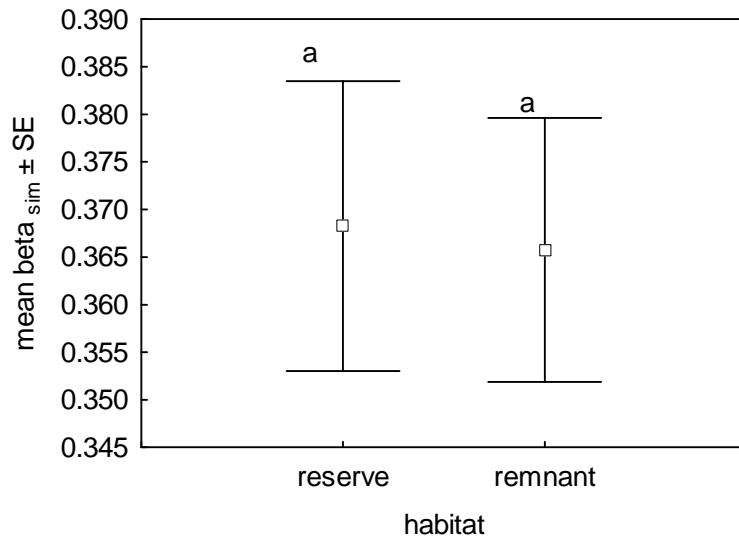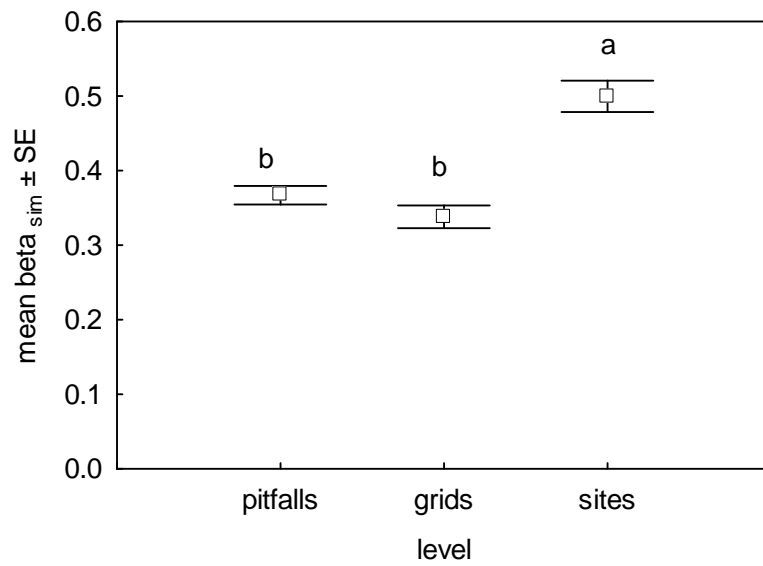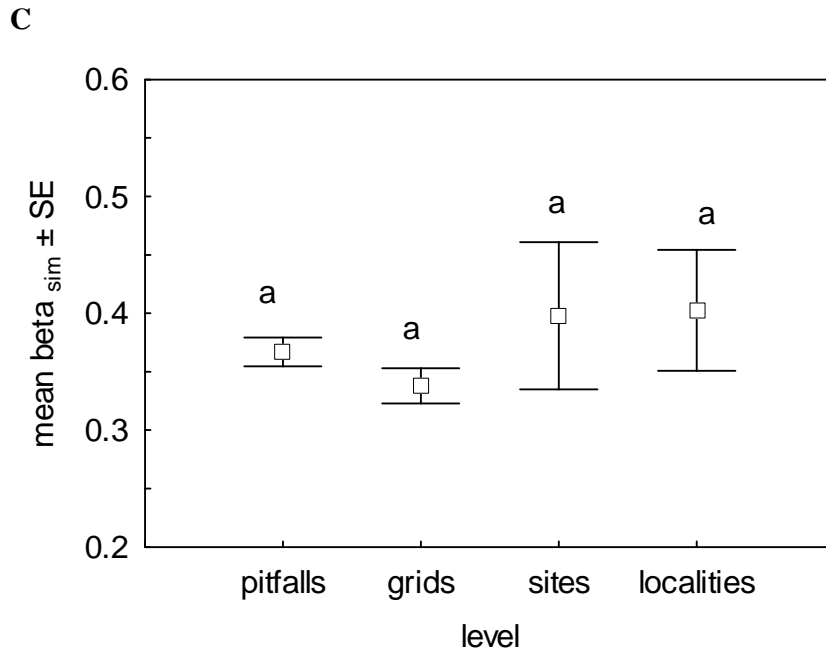
Figure 8 Compositional turnover (ßsim) **A**) for reserve and remnants, **B**) across three hierarchical levels, between pitfalls in grids, between grids within sites and between sites within the region   and **C**) across four hierarchical levels, between pitfalls in a grid, between grids in a site and between sites in a locality, between localities in the region. Note that scaling on the y-axis differs between graphs.

Appendix 1 Sampling sites and broad vegetation types (taken from the new vegetation map (Mucina & Rutherford 2004)) across the lowlands for the Cape Floristic Region. Slope is graded 1 – flat, 2 - gradual, 3 - intermediate, 4 - steep, 5 - very steep.

Locality	Sites	Plots	GPS Coordinates Decimal degrees (WGS 84)	Elevation	Aspect	Slope	Broad vegetation type
Elandskloofberge **EB**	Reserve (Elandsberg) **EBR**	1	33.43714 S, 19.03837 E	71	/	1	Swartland Alluvium Fynbos
		2	33.44709 S, 19.04528 E	85	/	1	Swartland Alluvium Fynbos
		3	33.44606 S, 19.05520 E	100	/	1	Swartland Shale Renosterveld
		4	33.44842 S 19.06482 E	132	W	2	Swartland Alluvium Fynbos
		5	33.45431 S, 19.06647 E	170	W	3	Swartland Alluvium Fynbos
	Remnants **EBF**	1	33.44815 S, 19.02773 E	103	/	1	Swartland Shale Renosterveld
		2	33.44345 S, 19.0294 E	79	/	1	Swartland Alluvium Fynbos
		3	33.44214 S, 19.02223 E	73	/	1	Swartland Shale Renosterveld
		4	33.45412 S, 19.01676 E	84	E	2	Swartland Shale Renosterveld
		5	33.45640 S, 19.02723 E	109	E	2	Swartland Shale Renosterveld

Locality	Sites	Plots	GPS Coordinates Decimal degrees (WGS 84)	Elevation	Aspect	Slope	Broad vegetation type
Malmesbury **MB**	Reserve (Riverlands) **MBR**	1	33.49324 S, 18.58664 E	110	/	1	Atlantis Sand Fynbos
		2	33.49283 S, 18.58384 E	112	/	1	Atlantis Sand Fynbos
		3	33.49489 S, 18.58316 E	110	/	1	Atlantis Sand Fynbos
		4	33.49764 S, 18.58674 E	108	/	1	Atlantis Sand Fynbos
		5	33.49426 S, 18.59241 E	96	/	1	Atlantis Sand Fynbos
	Remnants (Pella Nature Reserve) **MBF**	1	33.52153 S, 18.55004 E	126	/	1	Atlantis Sand Fynbos
		2	33.51969 S, 18.54834 E	150	/	1	Atlantis Sand Fynbos
		3	33.52008 S, 18.54624 E	162	/	1	Atlantis Sand Fynbos
		4	33.52212 S, 18.54572 E	168	SE	2	Atlantis Sand Fynbos
		5	33.52296 S, 18.54772 E	160	/	1	Atlantis Sand Fynbos

Locality	Sites	Plots	GPS Coordinates Decimal degrees (WGS 84)	Elevation	Aspect	Slope	Broad vegetation type
Grabouw GW	Reserve (Hottentots Holland) GWR	1	33.96367 S, 19.16108 E	339	W	2	Kogelberg Sandstone Fynbos
		2	33.9674 S, 19.15308 E	344	S	2	Kogelberg Sandstone Fynbos
		3	33.97699 S, 19.13786 E	338	SE	2	Kogelberg Sandstone Fynbos
		4	33.98328 S, 19.12955 E	353	/	1	Kogelberg Sandstone Fynbos
		5	33.9864 S, 19.13306 E	335	/	1	Kogelberg Sandstone Fynbos
	Remnants GWF	1	34.16872 S, 19.09512 E	359	SW	2	Elgin Shale Fynbos
		2	34.17307 S, 19.09923 E	339	SW	4	Elgin Shale Fynbos
		3	34.17519 S, 19.09379 E	318	NE	3	Elgin Shale Fynbos
		4	34.16449 S, 19.09379 E	381	NE	3	Elgin Shale Fynbos
		5	34.1604 S, 19.10625 E	376	SE	2	Elgin Shale Fynbos

Locality	Sites	Plots	GPS Coordinates Decimal degrees (WGS 84)	Elevation	Aspect	Slope	Broad vegetation type
Stellenbosch **STB**	Reserve (Jonkershoek) **STBR**	1	33.99158 S, 18.97195 E	382	SW	2	Boland Granite Fynbos
		2	33.99265 S, 18.97469 E	387	N	2	Boland Granite Fynbos
		3	33.99151 S, 18.96856 E	368	NE	4	Boland Granite Fynbos
		4	33.9906 S, 18.96525 E	342	N	2	Boland Granite Fynbos
		5	33.98968 S, 18.97099 E	366	SW	3	Boland Granite Fynbos
	Remnants **STBF**	1	33.92157 S, 18.72264 E	215	SW	4	Swartland Granite Renosterveld
		2	33.92367 S, 18.72826 E	309	W	2	Boland Granite Renosterveld
		3	33.92423 S, 18.73129 E	333	N	3	Boland Granite Renosterveld
		4	33.9189 S, 18.73094 E	214	NW	3	Swartland Granite Renosterveld
		5	33.92048 S, 18.72859 E	243	W	4	Swartland Granite Renosterveld

Locality	Sites	Plots	GPS Coordinates Decimal degrees (WGS 84)	Elevation	Aspect	Slope	Broad vegetation type
Somerset West **SW**	Reserve (Helderberg) **SWR**	1	34.06201 S, 18.87568E	163	SW	2	Lourensford Alluvium Fynbos
		2	34.05836 S, 18.87628 E	188	SW	2	Lourensford Alluvium Fynbos
		3	34.05591 S, 18.87609 E	210	SW	2	Lourensford Alluvium Fynbos
		4	34.05699 S, 18.86770 E	230	SE	3	Cape Winelands Shale Fynbos
		5	34.05565 S, 18.86949 E	232	E	3	Cape Winelands Shale Fynbos
	Remnants **SWF**	1	34.03158 S, 18.84770 E	285	SW	5	Cape Winelands Shale Fynbos
		2	34.03428 S, 18.84764 E	280	NW	4	Cape Winelands Shale Fynbos
		3	34.03267 S, 18.85042 E	280	NW	4	Cape Winelands Shale Fynbos
		4	34.03126 S, 18.85570 E	310	SW	5	Cape Winelands Shale Fynbos
		5	34.03109 S, 18.84216 E	260	NE	2	Swartland Granite Renosterveld

Appendix 2A Weather data for the 10 sites provided by AgroMet – ISCW Agricultural Research Council as well as the WRC, CSIR and WCNCB over the five day trapping periods at each site.

Site	Weather station	Dates sampled	Mean wind speed (m/s)	Total rain (mm)	Mean humidity (% relative humidity)
Elandskloofberge	Diemierskraal, Paarl (-33.35S; 18.55E)	6-10 Oct	2.26 ± 0.71	36 (4 days)	72.95 ± 9.04
Malmesbury	Skaapkraal, Malmesbury (-33.53S; 18.633E)	29 Oct – 3 Nov	not available	1.8 (1 day)	54.92 ± 4.47
Grabouw Reserve	LaMotte, Franschhoek (-33.88S; 19.072E)	28 Oct -2 Nov	2.08 ± 0.68	11.94 (1 day)	61.19 ± 8.68
Grabouw Remnant	Oak Valley, Grabouw (-34.16S; 19.06E)	27 Oct – 1 Nov	2.82 ± 0.84	3.5 (1 day)	63.98 ± 5.34
Stellenbosch Reserve	Alto, Stellenbosch (-34.02S;18.55E)	15-20 Oct	2.67 ± 1.33	0.4 (2 days)	64.12 ± 13.43
Stellenbosch Remnant	Jacobsdal, Kuilsrivier (-33.97S; 18.73E)	14-19 Oct	< 0.01	1.6 (2 days)	64.97 ± 9.55
Somerset West Reserve	Vergelegen, Somerset West (-34.08S; 18.90E)	13-18 Oct	2.0 ± 0.85	2.6 (4 days)	66.6 ± 6.60
Somerset West Remnant	Fleurbaix, Stellenbosch (-33.95S; 18.83E)	13-18 Oct	< 0.01	0	62.08 ± 3.64
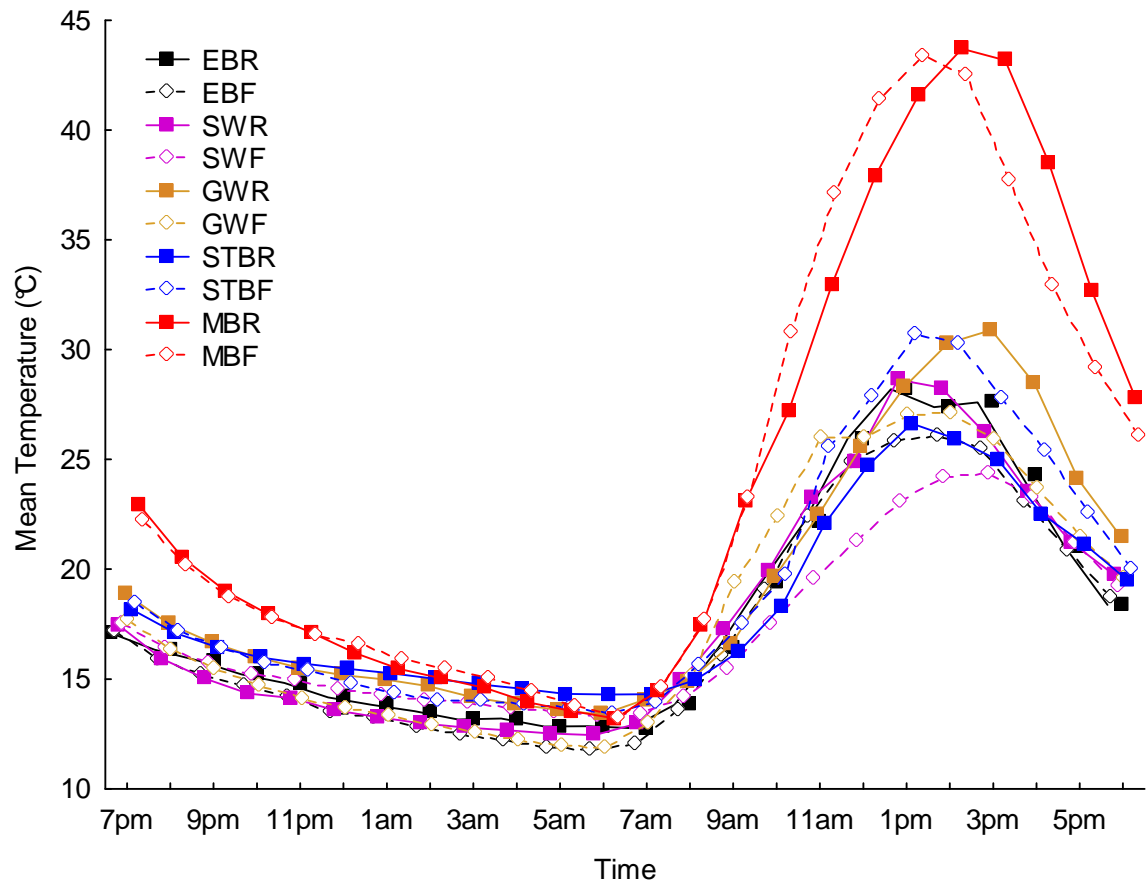
Appendix 2B Mean (n = 5 days) daily ground surface temperatures for all 10 sites. Paired sites are given in the same colours, with reserve sites (solid lines) and remnant sites (dotted lines). See Appendix 1 for site abbreviations.
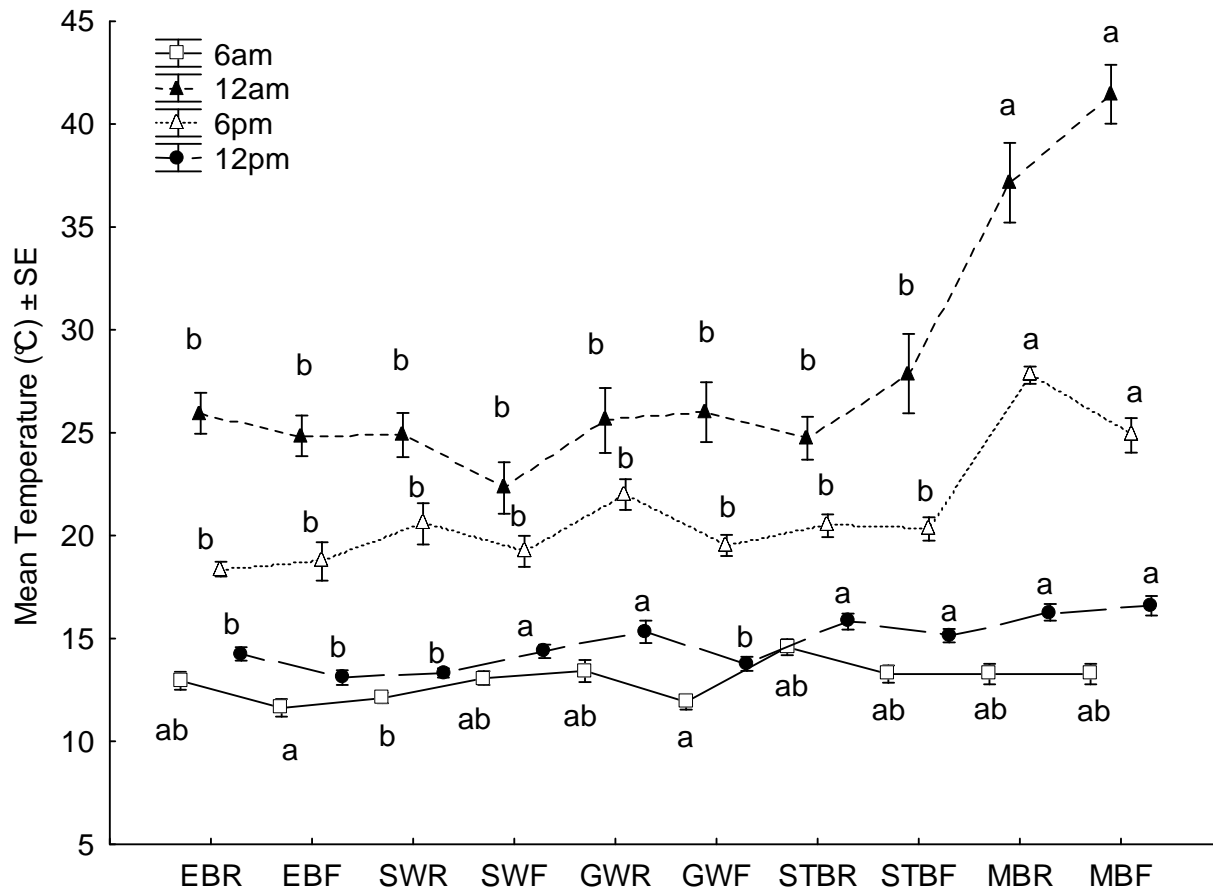
Appendix 2C Mean temperature (n = 5 days) for four time intervals, 6:00, 12:00, 18:00 and 24:00 for each of the 10 sites. The whiskers bearing the same letters indicate values that are not significantly different at the 5 % level. See Appendix 1 for site abbreviations.

Appendix 3A Soil variables (mean/median ± stdev/range) for 10 sites of five localities. Bold letters for each soil variables which do not have letters in common are significantly different across sites at $p < 0.05$. ***** indicates significant differences between paired sites.

Locality	Site	Mean Soil Resistance (Ohms)	Mean H^+ conc. (cmol/kg)	Median % N	Median % C
Elandskloofberge	Res	2462 ± 778 **ab**	1.2 ± 0.6 **ab**	0.04 ± 0.07 **ab**	1.35 ± 1.94 **ab**
	Rem	1476 ± 700 **ab**	1.0 ± 0.5 **ab**	0.06 ± 0.05 **ab**	1.64 ± 1.16 **ab**
Malmesbury	Res	3120 ± 1345 **ab**	0.6 ± 0.1 **b**	0.02 ± 0.01 **b**	0.40 ± 0.11 **b**
	Rem	3902 ± 466 **ac**	0.7 ± 0.1 **cb**	0.03 ± 0.01 **bc**	0.68 ± 0.37 **b**
Grabouw	Res	5596 ± 2005 **ac***	1.8 ± 1.2 **ab**	0.03 ± 0.14 **ab**	1.21 ± 6.31 **ab**
	Rem	848 ± 387 **b***	1.3 ± 0.6 **ab**	0.13 ± 0.06 **ac**	2.78 ± 2.53 **ab**
Stellenbosch	Res	4366 ± 718 **a**	2.0 ± 0.3 **ac**	0.07 ± 0.02 **ab**	2.13 ± 0.73 **ab**
	Rem	1594 ± 483 **ab**	1.3 ± 0.3 **ab**	0.12 ± 0.02 **ac**	2.68 ± 0.71 **ab**
Somerset West	Res	1804 ± 507 **ab**	2.9 ± 1.0 **a**	0.14 ± 0.07 **ac**	5.35 ± 1.98 **a**
	Rem	1312 ± 247 **bc**	1.3 ± 0.5 **ab**	0.17 ± 0.09 **a**	4.4 ± 2.31 **a**

		Exchangeable cations (mean)			
		Na	K	Ca	Mg
Elandskloofberge	Res	0.06 ± 0.05 **ab**	0.12 ± 0.10 **ab**	1.07 ± 0.52 **ab**	0.52 ± 0.36 **ab**
	Rem	0.21 ± 0.35 **ab**	0.16 ± 0.06 **ab**	1.41 ± 0.67 **ab**	0.70 ± 0.39 **ab**
Malmesbury	Res	0.06 ± 0.04 **bc**	0.04 ± 0.02 **b**	0.48 ± 0.06 **b**	0.16 ± 0.04 **b**
	Rem	0.04 ± 0.01 **bc**	0.04 ± 0.01 **b**	0.71 ± 0.33 **ab**	0.16 ± 0.04 **b**
Grabouw	Res	0.02 ± 0.01 **b***	0.04 ± 0.02 **b***	0.61 ± 0.38 **bc***	0.21 ± 0.13 **b***
	Rem	0.72 ± 0.52 **a***	0.46 ± 0.14 **a***	4.79 ± 1.21 **a***	2.39 ± 0.64 **a***
Stellenbosch	Res	0.05 ± 0.01 **ac**	0.13 ± 0.04 **b**	0.59 ± 0.23 **ab**	0.25 ± 0.08 **b**
	Rem	0.11 ± 0.03 **ab**	0.32 ± 0.06 **ab**	3.65 ± 0.38 **ac**	1.17 ± 0.15 **ab**
Somerset West	Res	0.17 ± 0.04 **ac**	0.30 ± 0.07 **ab**	2.27 ± 0.89 **ab**	1.26 ± 0.34 **ab**
	Rem	0.18 ± 0.10 **ac**	0.51 ± 0.19 **a**	5.28 ± 1.31 **a**	2.66 ± 1.26 **a**

		% Base saturation (median)			
		Na	K	Ca	Mg
Elandskloofberge	Res	1.8 ± 1.0 **ab**	3.73 ± 2.4 **ab**	37.8 ± 11.0 **ab**	16.29 ± 4.7 **ab**
	Rem	1.8 ± 21.8 **ab**	5.1 ± 2.9 **ab**	35.7 ± 30.0 **ab**	17.6 ± 16.7 **ab**
Malmesbury	Res	3.4 ± 6.5 **a**	3.1 ± 3.4 **ab**	36.0 ± 14.0 **ab**	11.62 ± 5.2 **ab**
	Rem	2.4 ± 2.9 **ab**	2.3 ± 1.5 **ab**	39.2 ± 21.4 **ab**	9.27 ± 2.57 **b**
Grabouw	Res	1.0 ± 0.7 **b***	1.7 ± 1.3 **b**	21.9 ± 14.6 **bc**	7.57 ± 2.92 **b***
	Rem	4.9 ± 13.8 **a***	4.8 ± 3.8 **ab**	49.4 ± 22.0 **ac**	23.1± 11.0 **a***
Stellenbosch	Res	1.7 ± 0.7 **ab**	3.9 ± 2.9 **ab**	16.5 ± 16.5 **b***	7.7 ± 5.6 **b**
	Rem	1.5 ± 0.9 **ab**	5.0 ± 1.6 **a**	54.9 ± 5.9 **a***	18.7 ± 4.9 **ab**
Somerset West	Res	2.7 ± 1.9 **ab**	3.9 ± 3.4 **ab**	34.0 ± 26.9 **ab**	19.4 ± 9.3 **ab**
	Rem	1.3 ± 3.0 **ab**	5.5 ± 3.5 **a**	49.9 ± 24.1 **a**	27.0 ± 16.8 **a**
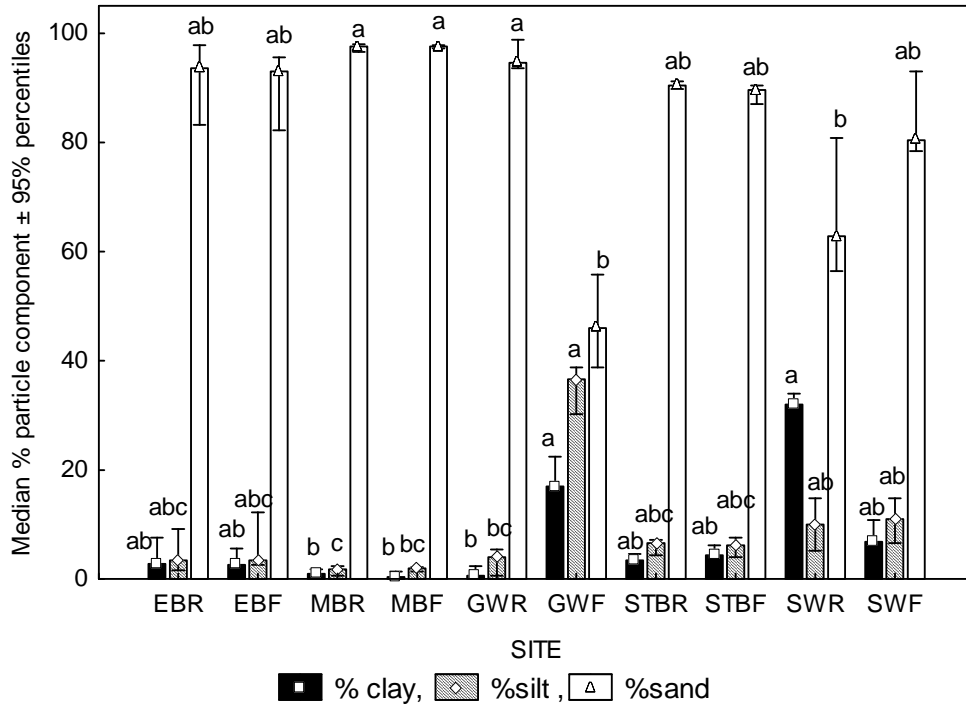
Appendix 3B Median percentage sand, silt and clay across each of the 10 sites. Bars bearing the same letters are not significantly different at the 5% level (n=5). See Appendix 1 for site abbreviations
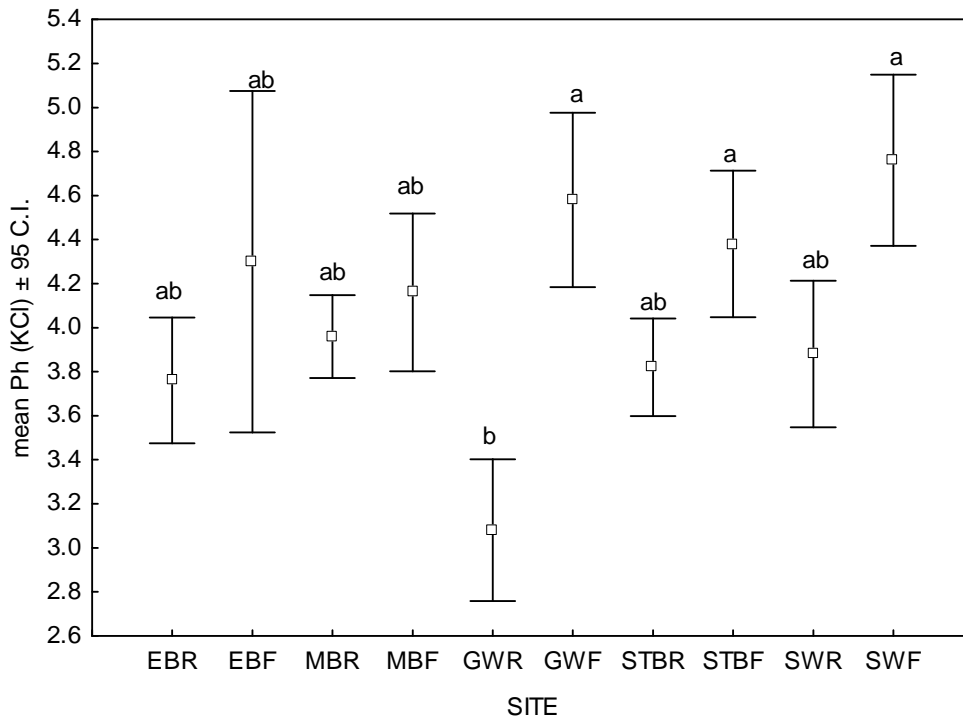
Appendix 3C Mean (± standard error) pH (KCl) across 10 sites (n = 5). Bars bearing the same letters are not significantly different at the 5% level. See Appendix 1 for site abbreviations.

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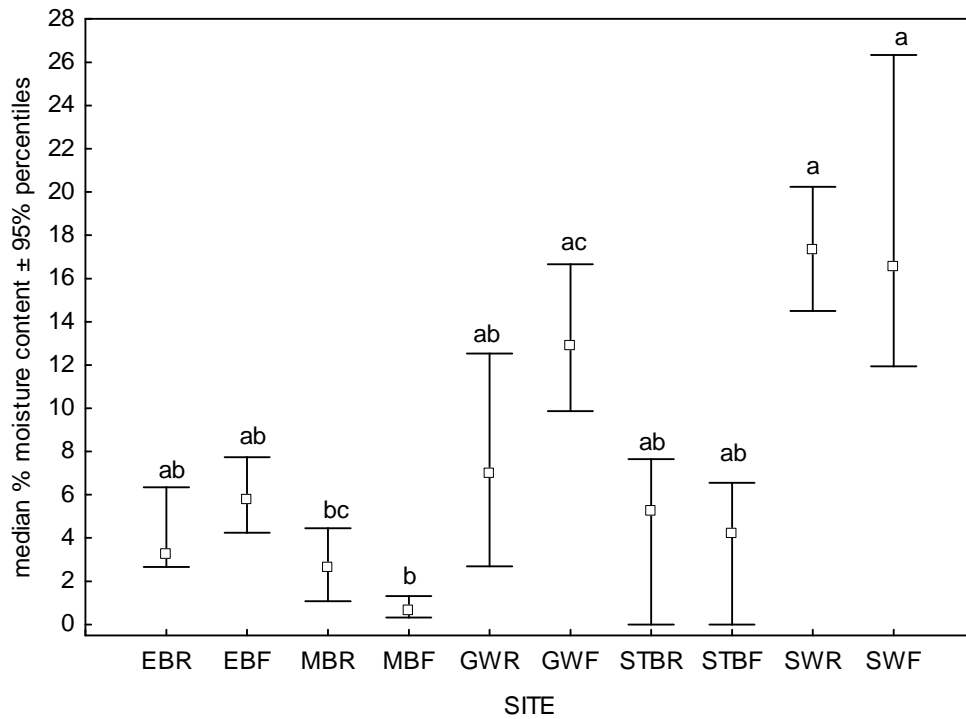
Appendix 3D Median % soil moisture content across 10 sites (n = 5). See Appendix 1 for site abbreviations. Bars bearing the same letters are not significantly different at the 5% level
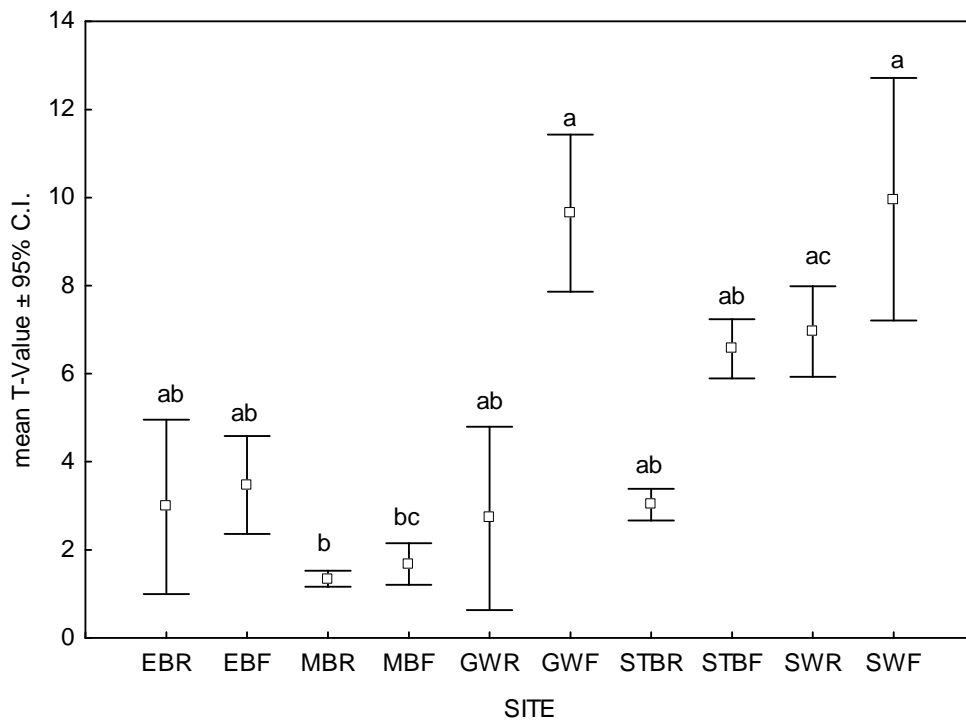
Appendix 3E Mean T-value (estimate of CEC-value) across ten sites (n = 5). Bars bearing the same letters are not significantly different at the 5% level. See Appendix 1 for site abbreviations.
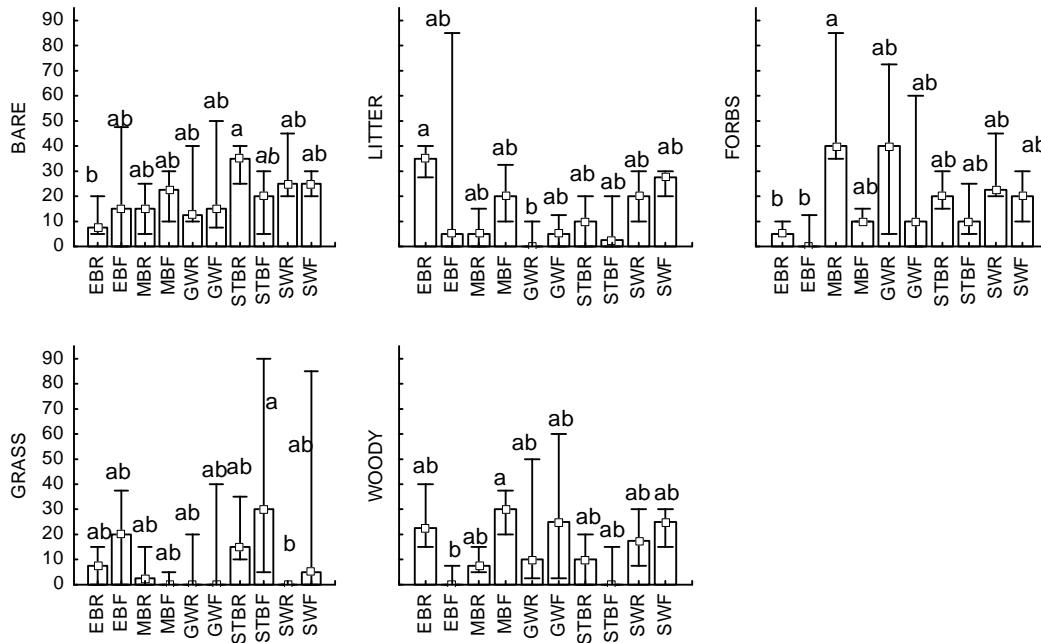
Appendix 4A: Median (± range) % vegetation cover for each of the ten sites (n = 50). Bars bearing the same letters were not significantly different at the 5% level. See Appendix 1 for site abbreviations.
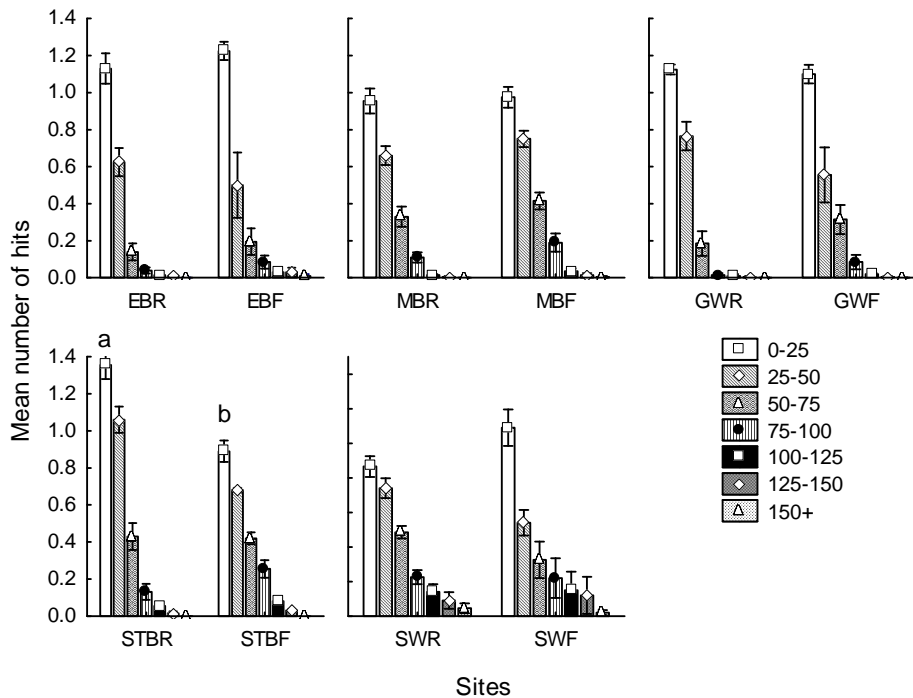
Appendix 4B Foliage Height Profiles (FHP) across the 10 sites (n = 50). Mean (± standard error) number of hits per height class (given in the legend) for paired sites. Letters were omitted when there were no significant differences at the 5% level between groups; otherwise different letters indicate significant differences between sites within a height class (p < 0.05). See Appendix 1 for site abbreviations.

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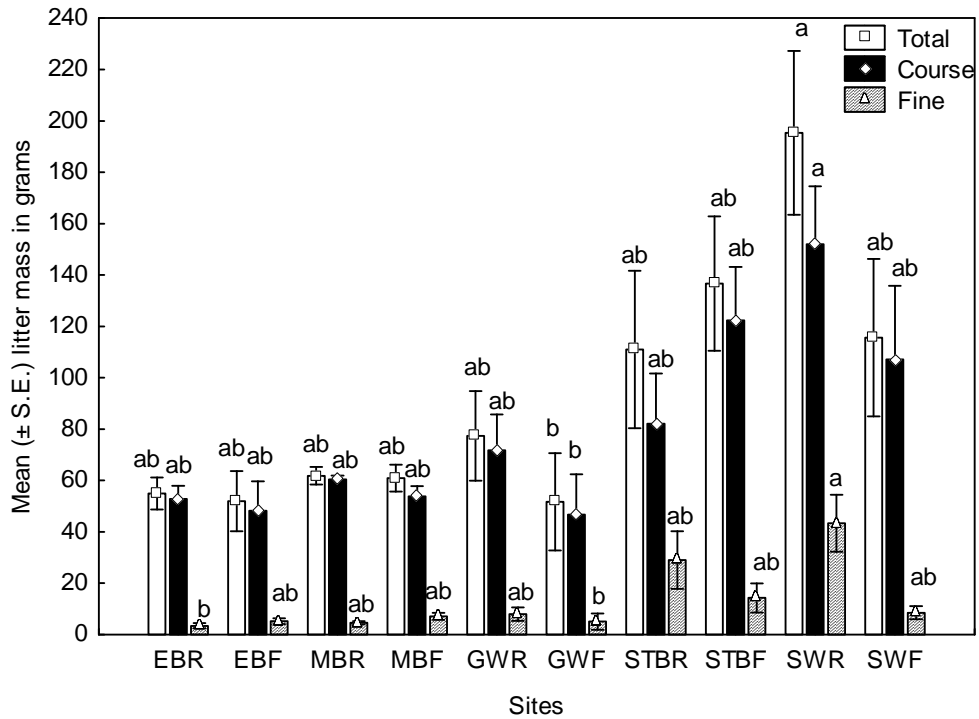
Appendix 4C Mean (± SE) weight of litter samples (n = 150), including total, course and fine weights across 10 sites. Bars having no letters in common indicate significant differences between sites at the 5% level within the total, course and fine. See Appendix 1 for site abbreviations.

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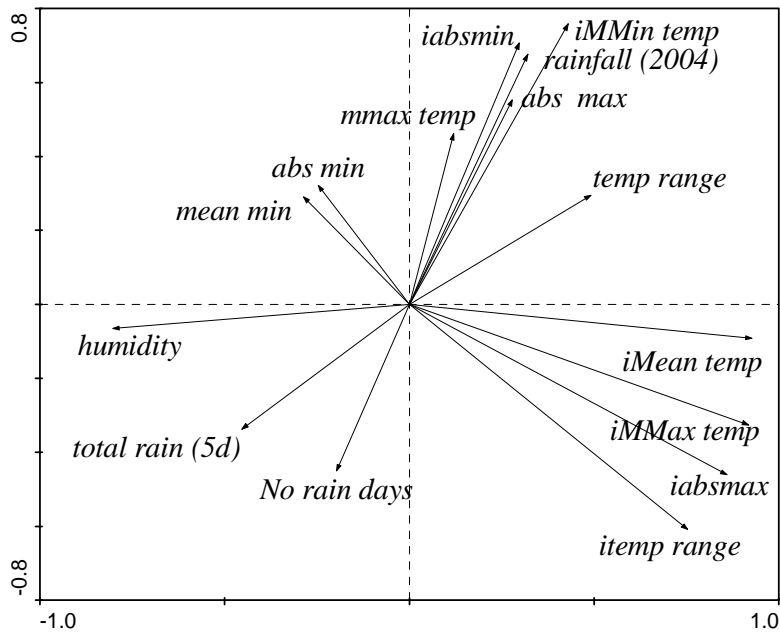
Appendix 5A PCA ordination plots of weather variables at site scale, number of days that rain fell during the 5 day sampling period (No rain days), total rainfall over the 5 day sampling period (total rain (5d)), total rainfall during 2004 (rainfall(2004)), mean relative humidity across 5 day sampling period (humidity), mean ambient temperatures in 2004: mean minimum (mean min), absolute min (abs min), mean maximum (mmax temp), absolute maximum (abs max), temperature range (temp range), ground temperatures: absolute minimum (iabsmin), mean minimum (iMMin temp), mean (iMean temp), mean maximum (iMMax temp), absolute maximum (iabs max) and temperature range (itemp range).
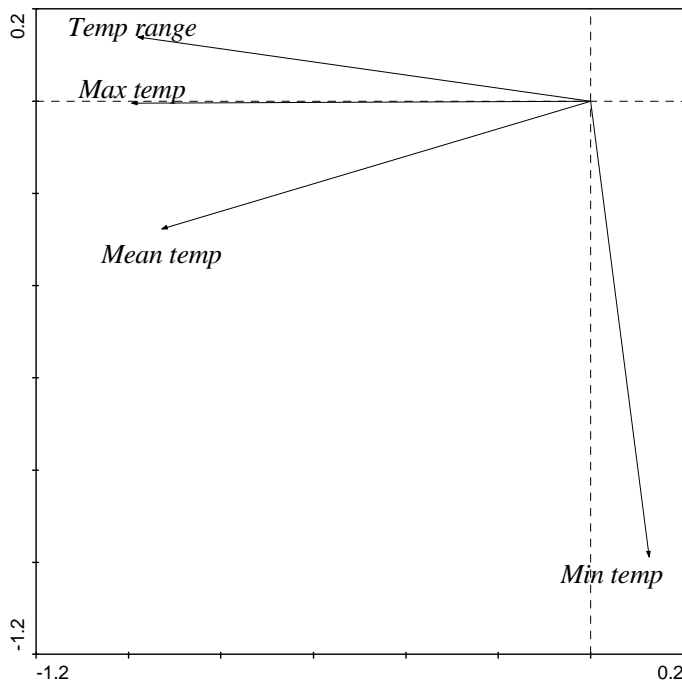
Appendix 5B PCA ordination plots of mean (n = 5 days) ground soil temperature variables, mean (mean temp), maximum (max temp), minimum (min temp) and range (temp range) using grid data.

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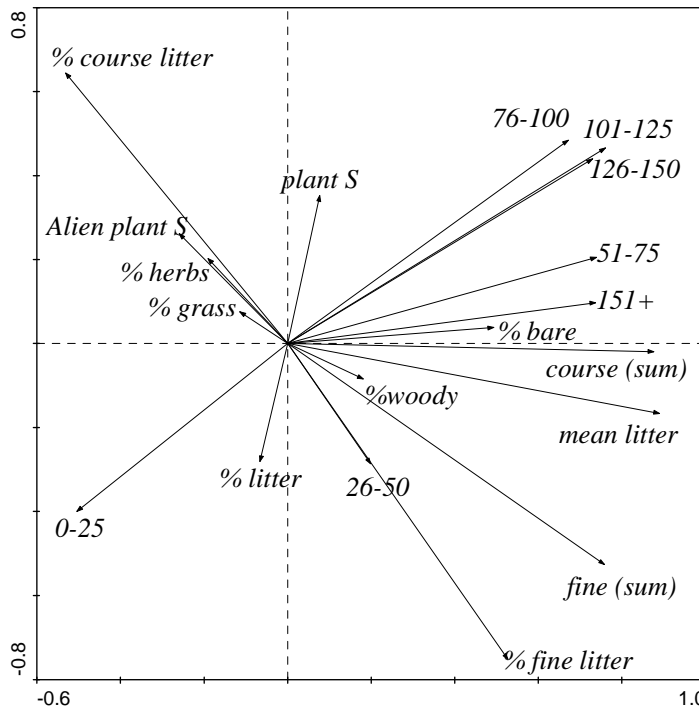
Appendix 5C PCA ordination plots of vegetation variables, using grid data, % cover: % bare, % grass, % litter, herbaceous component (% herbs) and % woody. Foliage height profiles: 0 – 0.25 m (0-25)…1.5 m and above (h150+), plant species richness (plant S), Alien plant species richness (Alien plant S). Litter: % course and % fine, total weight of fine litter (fine (sum)), total weight of course litter (course (sum)) and mean weight of litter (mean litter).
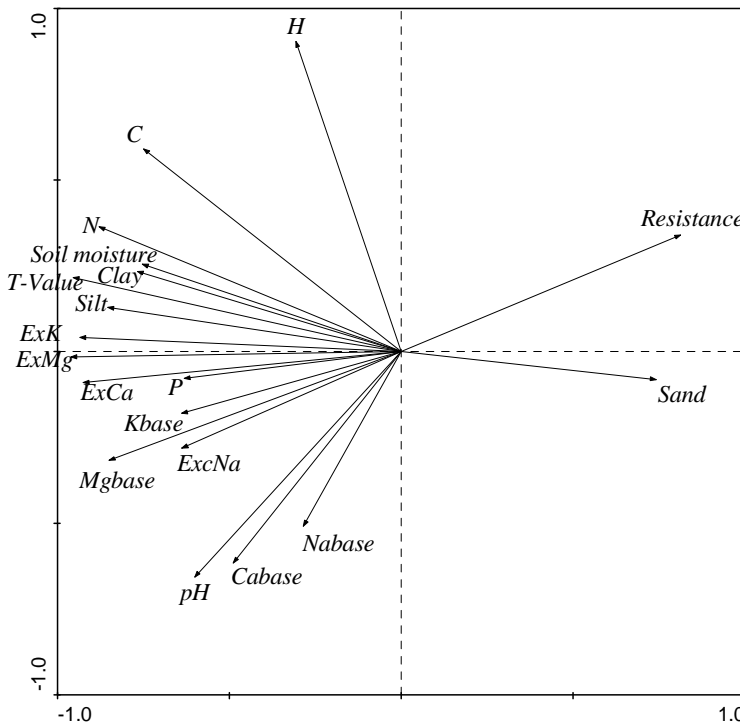
Appendix 5D PCA ordination plots of soil variables using grid data, soil moisture, soil resistance, H^+ concentration, pH, % sand, % silt and % clay composition, Nutrients, carbon (C), nitrogen (N), Phosphorus (P), exchangeable cations (ExMg, ExCa, ExK, ExNa) and % base saturation (Mgbase, Cabase, Kbase, Nabase).

Appendix 5E: Eigenvector coefficients (loadings) of a standardized principal component analysis of original environmental variables across 10 sites. Percentage variances explained by each axis is given in bold.

Site level	Variables used	Axis 1	Axis 2	Axis 3	Axis 4
Climate *	**% variance explained**	**31.6**	**22.3**	**20**	**14.1**
	Total rain (5-day)	-0.48	-0.45	-0.70	-0.21
	No. of rain days	-0.22	-0.45	-0.68	0.42
	Humidity (2004)	-0.80	-0.07	-0.47	0.26
	Rainfall (2004)	0.32	0.68	-0.37	0.38
	Mean max temp (2004)	0.09	0.47	-0.63	-0.42
	Abs max temp (2004)	0.29	0.55	-0.72	-0.22
	Mean min temp (2004)	-0.25	0.28	-0.00	-0.52
	Abs min temp (2004)	-0.24	0.32	0.04	-0.90
	Range temp (2004)	0.50	0.30	-0.75	0.20
	ground mean max temp (5- day)	0.92	-0.32	-0.05	-0.16
	ground mean min temp (5- day)	0.41	0.76	0.22	0.34
	ground abs max temp (5- day)	0.85	-0.46	-0.13	0.03
	ground min max temp (5- day)	0.25	0.71	0.31	0.32
	ground mean temp (5- day)	0.92	-0.09	0.05	-0.28
	ground temp range (5- day)	0.75	-0.60	-0.20	-0.03
Soil	**% variance explained**	**65.5**	**16.8**	**9.38**	**3.28**
	Soil moisture	0.82	0.44	0.03	0.10
	pH	0.70	-0.60	-0.21	-0.19
	Resistance	-0.92	0.34	-0.05	0.04
	H^+	0.31	0.92	0.10	-0.17
	P	0.69	-0.09	-0.59	-0.01
	Exchangeable Na	0.79	-0.23	0.53	0.15
	Exchangeable K	0.98	0.05	-0.13	0.03
	Exchangeable Ca	0.95	-0.06	-0.19	0.17
	Exchangeable Mg	0.98	-0.00	-0.11	0.13
	% N	0.93	0.31	-0.16	0.05
	% C	0.76	0.63	-0.16	-0.01
	% base saturation (Na)	0.38	-0.65	0.59	-0.12
	% base saturation (K)	0.77	-0.20	-0.10	-0.59
	% base saturation (Ca)	0.60	-0.65	-0.30	0.22
	% base saturation (Mg)	0.89	-0.29	-0.11	-0.01
	T-value	0.96	0.22	-0.10	0.08
	% Clay	0.87	0.28	0.28	-0.20
	% Silt	0.91	0.16	0.30	0.04
	% Sand	-0.78	-0.06	-0.58	-0.13
Vegetation	**% variance explained**	**42.9**	**21.7**	**17.6**	**7.1**
	Plant species richness	0.40	0.58	-0.58	0.28
	Alien plant species richness	0.05	-0.65	0.06	0.62
	% bare ground	-0.64	0.10	-0.59	-0.39
	% litter cover	0.66	-0.02	-0.62	-0.23
	% grass cover	-0.32	-0.59	0.50	-0.43
	% herb cover	-0.22	0.81	0.32	0.30
	% woody cover	0.51	0.18	-0.66	-0.14
	FHP 0-25cm	-0.47	0.30	0.79	0.12

FHP 26-50cm	0.35	0.91	0.19	0.06
FHP 51-75cm	0.87	0.23	-0.18	0.16
FHP 76-100cm	0.82	-0.23	-0.23	0.18
FHP 101-125cm	0.83	-0.43	0.21	0.18
FHP 126-150cm	0.65	-0.62	0.29	0.16
FHP 151+ cm	0.74	-0.44	0.22	-0.31
Mean litter	0.94	-0.04	0.08	-0.05
Course litter (total)	0.91	-0.14	0.00	0.01
Fine litter (total)	0.87	0.26	0.27	-0.25
% course litter	-0.65	-0.42	-0.51	0.20
% fine litter	0.64	0.52	0.48	-0.19

* Climate variables were taken either only for the period that sampling was conducted (5-day) or means from across the year (2004).

Appendix 5F: Eigenvector coefficients (loadings) of a standardized principal component analysis of original environmental variables across 50 grids belonging to 10 sites. Percentage variances explained by each axis is given in bold.

Grid level	Variables used	Axis 1	Axis 2	Axis 3	Axis 4
Climate	**% variance explained**	**70.6**	**26.8**	**2.5**	**0.1**
	Max ground temperature (5 –day)	-0.99	0.00	-0.141	0.04
	Min ground temperature (5 –day)	0.13	-0.99	-0.09	0.00
	Mean ground temperature (5–day)	-0.93	-0.28	0.25	-0.01
	Ground temperature range (5–day)	-0.98	0.14	-0.14	-0.04
Soil	**% variance explained**	**56.4**	**15.3**	**11.5**	**0.04**
	Soil moisture	-0.75	0.25	0.04	0.24
	pH	-0.60	-0.66	-0.24	-0.13
	Resistance	0.81	0.34	-0.27	-0.02
	H^+	-0.31	0.90	0.14	-0.11
	P	-0.63	-0.08	-0.56	0.12
	Exchangeable Na	-0.64	-0.28	0.64	0.18
	Exchangeable K	-0.94	0.04	-0.17	-0.12
	Exchangeable Ca	-0.93	-0.09	-0.25	0.14
	Exchangeable Mg	-0.96	-0.01	-0.10	0.11
	N	-0.88	0.36	-0.16	0.09
	C	-0.75	0.59	-0.14	0.02
	%base saturation (Na)	-0.28	-0.51	0.75	0.00
	%base saturation (K)	-0.64	-0.18	-0.18	-0.68
	%base saturation (Ca)	-0.49	-0.62	-0.42	0.14
	%base saturation (Mg)	-0.85	-0.32	-0.09	0.02
	T-value	-0.95	0.22	-0.09	0.09
	%Clay	-0.77	0.23	0.29	-0.28
	%Silt	-0.85	0.13	0.23	0.00
	%Sand	0.74	-0.08	-0.49	0.03
Vegetation	**% variance explained**	**31.8**	**13.5**	**13.1**	**8.6**
	plant species richness	0.08	0.35	-0.66	0.37
	alien plant species richness	-0.26	0.26	0.43	0.20
	% bare ground	0.49	0.04	-0.36	-0.23
	% litter cover	-0.07	-0.28	0.69	-0.05
	% grass cover	0.11	0.08	0.45	0.61
	% herb cover	-0.19	0.20	-0.48	0.43
	% woody cover	0.18	-0.08	-0.18	-0.79
	FHP 0-25cm	-0.50	-0.40	0.06	-0.02
	FHP 26-50cm	0.20	-0.29	-0.66	0.06
	FHP 51-75cm	0.74	0.21	-0.32	-0.06
	FHP 76-100cm	0.67	0.48	0.07	0.02
	FHP 101-125cm	0.76	0.47	0.28	-0.01
	FHP 126-150cm	0.73	0.44	0.29	-0.16
	FHP 151+ cm	0.74	0.10	0.28	-0.12
	Mean litter	0.89	-0.17	0.04	0.22
	Course litter (total)	0.88	-0.02	0.06	0.22
	Fine litter (total)	0.76	-0.53	-0.06	0.22
	% course litter	-0.53	0.64	-0.13	-0.01
	% fine litter	0.53	-0.75	-0.03	0.16

Appendix 5G: Eigenvector coefficients (loadings) of a standardized principal component analysis of original environmental variables across 50 grids belonging to 10 sites. Cumulative percentage variances explained by each axis is given in bold. Climate data gives ground surface temperature across the five-day sampling period.

	Elandskloofberge				Malmesbury				Grabouw				Stellenbosch				Somerset West			
	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4
CLIM *																				
Max temp	0.98	-0.14	0.12	-0.03	-0.97	0.16	0.16	-0.01	-0.98	-0.16	0.05	0.04	-0.98	-0.10	-0.15	0.01	-0.99	0.10	0.06	-0.04
Min temp	0.60	-0.78	0.18	0.01	0.65	0.75	0.08	0.00	-0.34	0.94	0.05	-0.01	0.64	-0.76	-0.12	-0.00	0.44	0.90	0.05	0.00
Mean temp	0.50	-0.85	-0.18	0.00	-0.90	0.34	-0.27	0.00	-0.98	0.16	-0.13	0.00	-0.86	-0.46	0.23	-0.00	-0.93	0.32	-0.16	0.00
Temp range	0.99	0.09	0.07	0.03	-0.99	0.02	0.14	0.01	-0.94	-0.34	0.06	-0.04	-0.99	0.00	-0.14	-0.02	-0.99	-0.00	0.12	0.04
% var	**64.1**	**97.9**	**100**	**100**	**79.1**	**96.9**	**100**	**100**	**73.2**	**99.2**	**99.9**	**100**	**77.5**	**97.3**	**100**	**100**	**75.8**	**98.7**	**99.9**	**100**
SOIL																				
Soil moist	*0.84*	0.37	-0.33	0.31	*0.78*	-0.10	0.46	0.30	-0.77	0.19	-0.36	0.36	0.38	0.43	0.08	0.48	-0.00	-0.34	-0.83	-0.19
pH	0.29	0.58	-0.87	-0.03	-0.08	0.74	0.02	-0.08	-0.92	-0.31	0.20	-0.08	0.88	0.32	-0.13	-0.13	-0.90	0.40	-0.03	0.06
Resist.	-0.58	-0.70	0.57	-0.58	-0.87	-0.46	-0.04	-0.06	0.94	0.10	0.24	0.17	-0.95	0.22	-0.03	0.16	0.52	0.53	-0.08	-0.38
H^+	0.32	-0.62	0.01	0.89	-0.48	0.69	-0.07	0.15	0.16	0.95	-0.19	-0.02	-0.81	-0.43	0.22	0.21	0.92	-0.31	0.08	-0.04
P	0.45	-0.11	-0.39	-0.60	-0.63	0.50	-0.51	-0.07	-0.80	0.27	0.34	-0.20	0.94	-0.14	0.14	0.04	-0.83	0.16	-0.31	-0.16
Exc. Na	0.32	0.67	-0.41	-0.48	0.77	0.55	-0.13	0.08	-0.82	-0.28	-0.42	-0.24	0.85	-0.39	0.12	-0.18	0.10	-0.79	-0.43	0.26
Exc. K	0.92	-0.36	0.65	-0.34	0.63	0.74	0.08	-0.16	-0.94	0.04	0.10	0.22	0.97	0.03	-0.14	-0.14	-0.83	-0.36	0.32	0.24
Exc. Ca	0.88	-0.21	-0.06	0.21	-0.51	0.38	0.72	-0.24	-0.98	0.06	0.15	-0.09	0.99	-0.00	-0.04	0.04	-0.93	0.07	0.03	-0.23
Exc. Mg	0.93	0.28	0.25	0.36	0.31	0.63	0.63	0.03	-0.97	0.09	0.08	0.07	0.99	0.00	0.04	-0.03	-0.89	-0.37	0.22	-0.09
N	0.86	-0.43	0.43	0.32	-0.60	0.53	-0.06	0.20	-0.79	0.59	-0.06	0.04	0.96	-0.03	-0.04	0.19	-0.54	-0.59	-0.20	-0.41
C	0.61	-0.47	-0.15	0.18	-0.69	0.54	-0.14	0.26	-0.47	0.86	0.04	-0.07	0.72	-0.40	0.05	-0.06	0.40	-0.69	0.21	-0.36
%base sat Na	0.21	0.89	-0.14	-0.24	0.80	0.36	-0.28	0.14	-0.85	-0.37	-0.36	-0.15	-0.07	-0.70	0.39	-0.51	0.57	-0.55	-0.39	0.36
%base sat K	0.54	-0.52	-0.19	-0.27	0.80	0.44	-0.27	-0.08	-0.89	-0.19	0.07	0.35	0.47	0.47	-0.23	-0.42	-0.45	-0.22	0.32	0.74
%base sat Ca	0.11	-0.25	0.22	-0.18	-0.59	-0.07	0.66	-0.27	-0.90	-0.24	0.27	-0.09	0.96	0.15	-0.06	0.03	-0.82	0.29	-0.06	-0.09
%base sat Mg	0.61	0.71	0.38	-0.15	0.89	0.06	0.21	0.20	-0.97	-0.03	0.07	0.11	0.97	0.20	0.10	-0.05	-0.85	-0.34	0.24	0.14

* Climate data gives ground surface temperature across the five-day sampling period.

	Elandskloofberge				Malmesbury				Grabouw				Stellenbosch				Somerset West			
	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4
SOIL																				
%Clay	*0.73*	-0.35	-0.18	-0.23	0.59	-0.36	0.38	-0.29	-0.94	-0.24	0.04	0.09	0.58	-0.03	0.62	0.39	0.75	-0.04	0.55	-0.08
%Silt	*0.73*	0.16	-0.43	0.05	-0.52	0.10	0.14	0.72	-0.98	0.12	0.00	-0.10	-0.01	-0.48	-0.87	0.07	0.12	0.48	-0.38	0.42
%Sand	*-0.87*	0.11	-0.41	-0.08	-0.08	0.43	-0.59	-0.52	0.97	0.12	0.04	-0.05	-0.52	0.55	0.31	-0.51	-0.84	0.17	-0.35	0.16
% var	**45.3**	**69.3**	**87.7**	**94.6**	**38.7**	**62.8**	**78.2**	**85.4**	**74.8**	**89**	**93.2**	**96.1**	**63.5**	**75**	**83.4**	**90.1**	**48.8**	**66.2**	**77.4**	**86.6**
VEG																				
Plant S	0.22	-0.84	0.34	-0.14	-0.54	-0.21	-0.11	0.34	-0.40	0.14	0.79	-0.24	-0.79	-0.10	-0.23	-0.48	0.03	-0.03	-0.36	0.74
Alien plant S	-0.55	0.75	0.04	-0.06	-0.48	-0.26	0.11	0.81	-0.51	-0.19	-0.76	-0.08	-0.72	0.56	-0.01	-0.21	-0.86	0.22	0.27	-0.03
% bare ground	0.65	0.39	0.19	-0.59	0.19	-0.02	-0.91	0.12	-0.26	-0.76	-0.06	0.02	0.80	-0.25	-0.18	-0.09	0.72	0.42	-0.57	0.24
% litter	-0.38	0.12	-0.59	0.53	0.96	0.11	0.09	0.03	0.77	-0.22	-0.32	-0.25	0.53	0.22	-0.51	0.20	-0.41	0.12	0.80	0.28
% grass	-0.21	0.05	0.84	0.22	-0.34	-0.13	-0.54	-0.09	-0.25	0.70	-0.40	0.36	-0.67	0.25	0.62	-0.20	-0.57	0.28	0.70	0.24
% herb	0.65	-0.23	-0.45	-0.52	-0.81	0.02	0.57	0.00	-0.58	0.46	0.46	-0.15	0.48	-0.64	-0.16	0.40	-0.10	-0.74	-0.45	-0.38
% wood	0.5	-0.77	-0.49	-0.23	0.84	-0.29	-0.23	-0.02	0.79	-0.44	-0.26	-0.17	0.35	-0.19	-0.68	-0.40	0.88	0.00	-0.09	0.34
FHP 1	- 0.07	0.35	-0.52	0.45	0.16	-0.26	0.79	-0.38	0.14	0.83	0.01	-0.28	0.34	-0.91	0.17	-0.07	-0.93	-0.07	0.06	0.12
FHP 2	0.74	-0.31	0.27	0.14	0.59	-0.17	0.51	0.52	0.59	-0.24	0.58	-0.45	0.25	-0.87	0.01	-0.11	0.07	-0.96	0.03	0.02
FHP 3	0.79	0.14	0.32	0.41	0.59	-0.35	-0.07	0.57	0.69	-0.42	-0.26	-0.45	-0.14	-0.19	-0.86	-0.11	0.95	0.20	-0.05	0.05
FHP 4	0.75	0.24	0.23	0.52	0.70	-0.49	0.06	0.16	0.55	0.32	-0.60	-0.36	-0.52	0.30	-0.66	-0.11	0.57	0.73	-0.04	0.26
FHP 5	0.85	0.33	0.29	-0.08	0.43	-0.86	0.14	-0.05	0.31	0.71	-0.44	-0.26	-0.92	-0.17	0.20	-0.22	0.72	0.68	0.15	0.03
FHP 6	0.76	0.41	-0.12	-0.29	0.53	-0.60	0.15	-0.36	0.53	0.54	-0.14	-0.33	-0.26	0.33	-0.01	0.74	0.71	0.63	0.07	-0.15
FHP 7	0.74	0.49	-0.13	-0.32	0.70	-0.31	0.46	-0.10									0.78	0.08	0.45	-0.09
Mean litter	0.89	-0.01	-0.21	0.39	0.34	0.85	0.15	-0.03	0.88	0.22	0.26	0.31	0.54	0.83	-0.03	-0.07	0.92	-0.17	0.19	-0.20
Course litter (T)	0.91	-0.07	-0.20	0.33	-0.15	0.75	0.54	0.14	0.85	0.26	0.28	0.32	0.34	0.91	-0.11	-0.01	0.91	0.03	0.12	-0.28
Fine litter (T)	0.41	0.74	-0.16	-0.19	0.65	0.69	0.01	0.19	0.95	0.01	0.17	0.17	0.87	0.38	0.16	-0.18	0.73	-0.60	0.30	0.05
% course litter	0.23	-0.76	-0.13	0.09	-0.67	-0.32	0.48	0.26	-0.57	0.19	0.47	-0.52	-0.88	0.00	-0.31	0.31	-0.54	0.68	-0.32	-0.36
% fine litter	-0.50	0.85	-0.09	0.04	0.68	0.51	-0.06	0.27	0.85	-0.18	0.41	-0.06	0.88	0.00	0.31	-0.31	0.54	-0.68	0.32	0.36
% var	**39.8**	**63.5**	**75.6**	**86.8**	**33.5**	**57.1**	**73.4**	**83.0**	**41.2**	**60.2**	**77.9**	**86.9**	**38.1**	**65.2**	**79.4**	**87.6**	**49.6**	**71.8**	**85.6**	**93.3**

Appendix 6 Ant species occupancy across 5 localities' (EB = Elandskloofberge, MB= Malmesbury, GW = Grabouw, STB= Stellenbosch and SW = Somerset West) sites (Res= reserve, Rem = Remnant), within the lowland Cape Floristic Region. Presence of species in site is indicated by X. CS = cryptic species, HCS= Hot climate specialist, TCS = Tropical Climate Specialists, DD = Dominant Dolichoderinae, SC= Subordinate Camponitini, SP = Specialized Predators, OPP = Opportunist and GM = Generalized Myrmicinae (Functional Group (FG)'s given by C.L. Parr)

Species	abrev	EB		MB		GW		STB		SW		# of sites present	FG (biology)
		Res	Rem	Res	Rem	Res	Rem	Res	Rem	Res	Rem		
Aenictinae													
Aenictus rotundatus (Mayr) [X]	Aen1							X				1	TCS
Cerapachyinae													
Cerapachys sp.1	Cer1	X							X			2	SP
Cerapachys sp.2	Cer2								X			1	SP
Cerapachys sp. 3	Cer3									X		1	SP
Dolichoderinae													
Tapinoma sp.1	Tap1			X	X	X						3	OPP
Tapinoma sp.2	Tap2							X				1	OPP
Tapinoma sp.3	Tap3								X			1	OPP
Technomyrmex albipes (F.Smith) ? *[X]	Talb	X	X			X		X		X		5	OPP
Technomyrmex sp.1	Tec1					X		X		X	X	4	OPP
Linepithema humile (Mayr) *°[X]	Lhum					X	X	X		X	X	5	DD
Dorylus helvolus (Linneaus) [X]	Dor1					X		X				2	TCS
Formicinae													

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Species	abrev	EB Res	EB Rem	MB Res	MB Rem	GW Res	GW Rem	STB Res	STB Rem	SW Res	SW Rem	# of sites present	FG (biology)
Anoplolepis custodiens (F.Smith) [X]	Acus			X				X				2	HCS
Anoplolepis steingroeveri (Forel) [X]	Aste	X	X			X				X		4	HCS
Anoplolepis sp.1	Ano1		X									1	HCS
Camponotus sp.1 (*emarginatus* gp)	Cam1	X	X	X	X	X		X				6	SC
Camponotus sp.2	Cam2	X	X									2	SC
Camponotus vestitus (F. Smith)	Cves		X					X				2	SC
Camponotus mystaceus (Emery)	Cam4	X	X		X							3	SC
Camponotus sp.5	Cam5			X	X			X				3	SC
Camponotus (*maculates* gp)	Cmac			X	X	X	X	X				5	SC
Camponotus angusticeps (Emery)	Cang			X	X							2	SC
Camponotus niveosetosus (Forel)	Cniv			X	X	X		X				4	SC
Camponotus sp.11	Cam11							X		X	X	3	SC
Camponotus sp.12	Cam12		X									1	SC
Camponotus sp.13	Cam13		X		X	X						3	SC
Camponotus sp.14	Cam14				X		X					2	SC
Lepisiota sp.1	Lep1		X	X	X	X						4	OPP
Lepisiota sp.2	Lep2	X	X	X	X	X	X	X	X			8	OPP
Lepisiota sp.3	Lep3		X	X	X	X		X				5	OPP
Lepisiota sp.4	Lep4	X	X	X	X							4	OPP
Lepisiota sp.5	Lep5		X	X	X	X						4	OPP

Species	abrev	EB		MB		GW		STB		SW		# of sites present	FG (biology)
		Res	Rem	Res	Rem	Res	Rem	Res	Rem	Res	Rem		
Lepisiota sp.6	Lep6			X								1	OPP
Lepisiota sp.7	Lep6			X								1	OPP
Lepisiota sp.8	Lep8				X							1	OPP
Lepisiota sp.9	Lep9					X		X				2	OPP
Plagiolepis sp.1	Pla1		X	X		X	X	X	X	X	X	8	CS
Myrmicinae													
Cardiocondyla sp.1	Car1		X		X							2	OPP
Crematogaster sp.1	Cre1	X	X						X			3	GM
Crematogaster sp.2	Cre2			X					X			2	GM
Meranoplus peringueyi (Emery)	Mper					X	X		X	X	X	5	HCS
Messor sp.1	Mes1		X									1	HCS
Messor capensis (Mayr) [X]	Mcap	X	X				X	X				4	HCS
Monomorium sp.1	Mon1	X		X			X	X	X			5	GM
Monomorium sp.2 (*monomorium* gp)	Mon2	X	X			X	X	X	X	X	X	8	GM
Monomorium sp.3 (*monomorium* gp)	Mon3			X								1	GM
Monomorium sp.4	Mon4	X	X	X	X				X			5	GM
Monomorium sp.5	Mon5		X									1	GM
Monomorium havilandi (Forel) [X]	Mon6	X					X		X			3	GM
Monomorium sp.7	Mon7					X				X		2	GM
Monomorium sp.8 (*salomonis* gp)	Mon8	X	X	X	X	X	X	X		X	X	9	GM

Species	abrev	EB		MB		GW		STB		SW		# of sites present	FG (biology)
		Res	Rem	Res	Rem	Res	Rem	Res	Rem	Res	Rem		
Monomorium sp.10 (*monomorium* gp)	Mon10							X				1	GM
Monomorium sp.11	Mon11		X						X			2	GM
Monomorium sp.12	Mon12			X					X			2	GM
Monomorium sp.13	Mon13			X	X			X				3	GM
Monomorium sp.14	Mon14			X	X							2	GM
Monomorium sp.15	Mon15					X						1	GM
Monomorium fridae (Forel)	Mon16					X						1	GM
Oligomyrmex sp.1	Oli1						X					1	CS
Ocymyrmex sp.1	Ocy1	X	X	X					X			4	HCS
Ocymyrmex sp.2	Ocy2	X	X	X	X	X		X	X	X	X	9	HCS
Pheidole sp.1	Phe1	X	X	X	X	X		X				6	GM
Pheidole sp.2	Phe2	X	X	X	X	X		X				6	GM
Rhoptromyrmex sp.1	Rho1	X				X		X			X	4	OPP
Solenopsis sp.1	Sol1		X	X	X	X			X	X	X	7	CS
Solenopsis sp.2	Sol2	X			X			X				3	CS
Tetramorium sp.1	Tet1	X	X									2	HCS
Tetramorium quadrispinosum (Emery)[X]	Tqua	X	X	X	X	X	X	X	X	X	X	10	OPP
Tetramorium frigidum (Arnold) [X]	Tet3	X	X			X	X	X	X	X	X	8	OPP
Tetramorium sp.5 (*simillimum* gp)	Tet5		X				X	X		X		4	OPP
Tetramorium sp.7 (*smillimum* gp)	Tet7	X	X			X		X		X		5	OPP

Species	abrev	EB		MB		GW		STB		SW		# of sites present	FG (biology)
		Res	Rem	Res	Rem	Res	Rem	Res	Rem	Res	Rem		
Tetramorium sp.8 (?smillimum gp)	Tet8				X	X	X	X	X	X	X	7	OPP
Tetramorium sp.9 (*smillimum* gp)	Tet9		X			X	X	X	X	X	X	7	OPP
Tetramorium erectum (Emery) [X]	Tet10					X	X	X	X	X	X	6	OPP
Tetramorium sp.11	Tet11					X				X	X	3	OPP
Tetramorium sp.12	Tet12						X		X	X	X	4	OPP
Tetramorium sp.13 (?smillimum gp)	Tet13					X						1	OPP
Tetramorium sp.14	Tet14									X		1	OPP
Tetramorium sp.15 (?smillimum gp)	Tet15							X				1	OPP
Tetramorium sp.16 (?smillimum gp)	Tet16			X	X							2	OPP
Ponerinae													
Anochetus levaillanti (Emery)	Ano1		X									1	SP
Hypoponera sp.1	Hyp1						X					1	CS
Pachycondyla berthoudi (Forel)	Pber	X										1	SP
Pachycondyla strigulosa (Emery)	Pstr				X							1	SP
Species Richness		26	36	30	29	34	25	34	23	22	18		

* = tramp species (Schultz & McGlynn 2000)
° = known invasive species (Schultz & McGlynn 2000)
[X] = known to forage in vineyards (Addison & Samways 2000)

Appendix 7 Diversity components calculated using additive partitioning of diversity (S) ($\gamma = \alpha + \beta$) across the hierarchically scaled sampling design, and mean β_{sim} (a multiplicative beta diversity index).

Diversity component	Mean S ± s.d.	Mean β_{sim} ± s.d.
ALL		
Within pitfalls β_1(n = 500)	4.19 ± 2.11	-
Between pitfalls β_2 (n = 500)	8.89 ± 2.11	0.388 ± 0.292
Between grids β_3 (n = 50)	14.42 ± 4.22	0.338 ± 0.160
Between sites β_4 (n = 10) within region	55.50 ± 6.11	0.500 ± 0.149
Between sites within localities (n = 10)	11.7 ± 6.11	0.398 ± 0.148
Between localities (n = 5) within region	43.8 ± 0.92	0.402 ± 0.172
RESERVE		
Within pitfalls β_1(n = 250)	4.21 ± 2.09	-
Between pitfalls β_2 (n = 250)	9.71 ± 2.09	0.381 ± 0.296
Between grids β_3 (n = 25)	15.28 ± 4.31	0.358 ± 0.177
Between sites β_4 (n = 5) within region	39.8 ± 5.22	0.505 ± 0.154
REMNANTS		
Within pitfalls β_1(n = 250)	4.17 ± 2.14	-
Between pitfalls β_2 (n = 250)	8.07 ± 2.14	0.396 ± 0.287
Between grids β_3 (n = 25)	13.56 ± 4.03	0.318 ± 0.139
Between sites β_4 (n = 5) within region	40.20 ± 7.05	0.520 ± 0.158

APPENDIX 8 Site photos of 10 sites across the lowland Cape Floristic Region

Elandskloofberg Nature Reserve

Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

Elandskloofberge Remnants
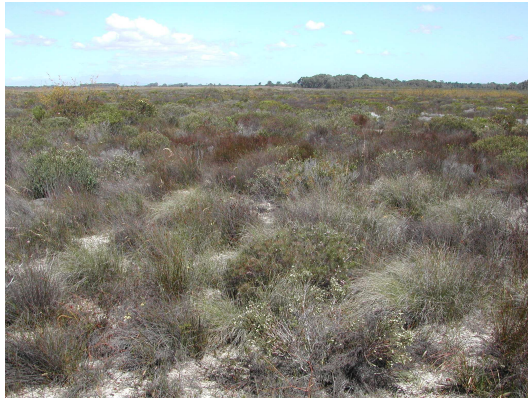
Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

Malmesbury Nature Reserve
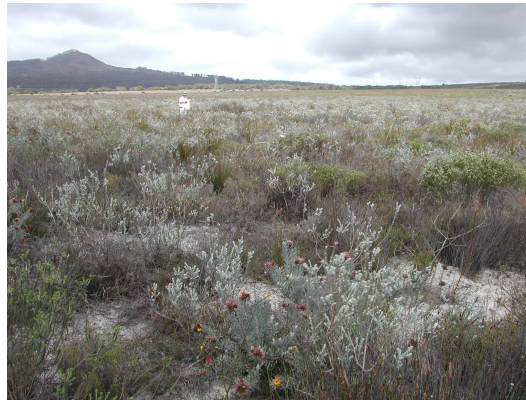
Grid1

Grid 2

Grid 3

Grid 4

Grid 5

Malmesbury Remnants

Grid 1

Grid 2

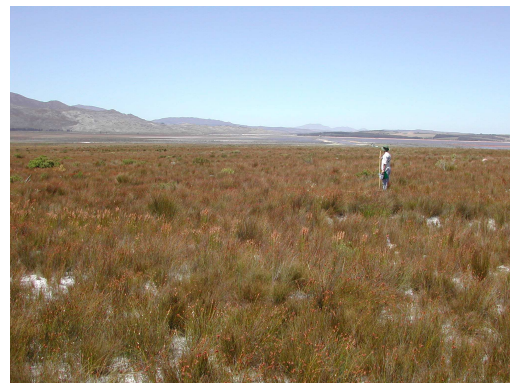
Grid 3

Grid 4

Grid 5

Grabouw Nature Reserve

Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

Grabouw Remnants

Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

Stellenbosch Nature Reserve

Grid 1

Grid2

Grid 3

Grid 4

Grid 5

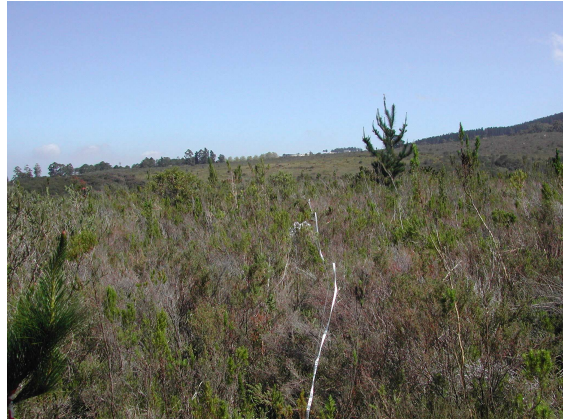Stellenbosch Remnants

Grid 1

Grid 2

Grid 3

Grid4

Grid 5

SomersetWest Nature Reserve

Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

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Somerset West Remnants

Grid 1

Grid 2

Grid 3

Grid 4

Grid 5

The conservation of biodiversity in natural and semi-natural remnants in human-influenced areas is essential (Knight 1999, Norton 2000, Goodman 2003, Solomon *et al.* 2003, Dudley *et al.* 2005). Although this concept is well understood in theory, the practical aspects, such as the magnitude of the contribution of remnants in regional biodiversity conservation is frequently unknown. This study investigated the contribution that remnants in the Cape Floristic Region (CFR) lowlands make to the overall conservation of this global biodiversity hotspot, by using ants as a flagship taxon.

Ants are a well studied taxon, particularly in Australia, where they have been used extensively in monitoring the environment (Andersen 1990, Bestelmeyer & Wiens 1996, Andersen 1997, Andersen *et al.* 2004, Andersen & Majer 2004). Although ants are not commonly used in environmental monitoring in South Africa, several studies have investigated the effects of various disturbances on ants (Donnelly & Giliomee 1985, Koen & Breytenbach 1988, Majer & Kock 1992, Tshiguvho *et al.* 1999, French & Major 2001, Fabricius *et al.* 2003, van Hamburg *et al.* 2004, Netshilaphala *et al.* 2005). The ant species richness of the CFR was estimated at about 100 species (Giliomee 2003). However this is likely to be a considerable underestimate, as this study which focused only on ground-foraging ant assemblages in the low-lying areas and only covered a relatively small part of the region's extent, already recorded 85 species. This study demonstrated that ants are an appropriate taxon to use as a flagship for epigaeic arthropod diversity in the CFR. They not only dominated the ground-dwelling fauna in the CFR (Chapter 2 & 3), but also reflected the seasonal fluctuations of the overall ground-dwelling arthropods (Chapter 3). Thus changes in ant assemblages have a broader relevance than to ants only, but reflect changes in ground-dwelling arthropods in general. Also, ants were found to be highly heterogeneous (Chapter 4), mirroring the well-known high heterogeneity of fauna and geology in the CFR (Cowling 1990). This highlights the conservation significance of ants and of arthropods in general in the CFR in addition to that of plants.

A key component of using ants as a flagship taxon is determining ways to maximize sampling efforts. Although many studies have focused on effective methods for sampling ants (Bestelmeyer *et al.* 2000, Lindsey & Skinner 2001, Parr & Chown 2001, James 2004), the aspect of whether to sample for longer or rather use more pitfall traps has not previously been looked at. This study found that increasing the spatial sampling intensity rather than increasing the sample duration maximized sampling efforts of ants in the CFR (Chapter 2). This adds a valuable aspect to the growing literature on effective ant sampling. Additionally this study found that sampling ants and ground-dwelling arthropods in general in the CFR was the most effective during summer (December) when ant species richness and abundance are highest (Chapter 3).

Finally, using ants, the contribution of remnants in the CFR lowlands to the regional conservation was investigated (Chapter 4). Overall, ant assemblages were similar between reserves and remnants, indicating the importance of remnants in the conservation of the CFR lowlands. More importantly however, this study highlighted that this potential is not necessarily realized. Several factors pose a distinct threat to the capacity of remnants to conserve ant assemblages, among them disturbances such as the presence of the Argentine ant and increasing soil nutrients by fertilizing. Additionally, beta diversity results suggested that not all remnants are always equally valuable and care should be taken in selecting remnants for conservation attention (Chapter 4). Furthermore, the future contribution of remnants to conservation is threatened by the fact that for the most part remnants occur on privately owned or communal land, and therefore have no official protection.

Although little successful progress has been made in managing or controlling the Argentine ant distribution since its introduction (Klotz *et al.* 2002, Soeprono & Rust 2004), great advances have been made for the formal protection of remnants in the CFR, by cooperative initiatives between nature conservation and the agricultural sector. A prime example is the Biodiversity and Wine Initiative (BWI) (Anonymous 2006). This initiative is a partnership between wine producers of the CFR and the conservation sector, which allows wine producers to enlist as members or champions, and thereby committing to conserving critical ecosystems and adopting biodiversity enhancing farming practices. In return wine producers benefit by amongst others using their membership as a unique marketing advantage. In August 2006, 29 % of the area covered by vineyard in the CFR was conserved (Anonymous 2006). This

study adds to the BWI by suggesting that in order to maximize conservation efforts, many farms are needed across the region, rather than conserving many remnants in a few farms.

This study highlighted the importance of remnants in ant assemblage conservation and gave some general guidelines, however more information will be needed before detailed management decisions can be made. Although ants in the CFR lowlands are known to occur in agricultural fields, such as vineyards (Addison & Samways 2000) and orchards (Witt & Samways 2004), the extent to which ants make use of and rely on various crops in between remnants is still unknown. This information will be needed to determine the effects of different land-use and agricultural practices on ant species foraging behaviour and their migration between remnants (Perfecto & Vandermeer 2002).

Although overall remnants support ant assemblages similar to those of the reserves, it is not clear whether they are able to support ant assemblages that were once present in the broader CFR. Comparisons to previous records are mostly not possible and species lists of ants for nature reserves or the larger region are generally non-existent. This study generated species lists for the various localities in the CFR (Chapter 4), as well as taxa level abundances for a single locality (Chapter 3), which will be useful for future monitoring programs in the area.

In conclusion, this study added valuable information to our knowledge of ant diversity patterns in the CFR lowlands, as an important basis both for sampling effectively and future monitoring. Further, the study showed that overall remnants support ant assemblages representative of those present in the CFR today. Therefore some remnants in human-influenced areas currently contribute highly to the conservation of this global biodiversity hotspot and if managed correctly, may continue to do so in the future.

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