The impact of land use on invertebrate assemblages in the Succulent Karoo, South Africa.

By

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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 Succulent Karoo biodiversity hotspot is threatened by pressure caused by increasing human populations and its associated land use types. Land use is primarily focussed on agriculture, with livestock grazing as a dominant land use in the region. Cultivation is also practiced along the major perennial rivers, and in drier areas, where this largely depends on rainfall. Only about seven percent of the biome is formally protected, and this area substantially under-represents the biodiversity of the Succulent Karoo and does not incorporate key ecological processes and biodiversity drivers. Therefore, there is urgent need for outside reserve conservation initiatives, whose success depend on understanding the ecosystem function of the Succulent Karoo. This study aimed to determine the impacts of heavy grazing, light grazing and cultivation (in a 30-year old fallow field) on assemblages of ground-dwelling and flying invertebrates. Seasonal assemblage changes were also determined. Vegetation structure and composition were determined using the line-intercept method to determine if vegetation patterns explain patterns in invertebrate assemblages. Abandoned fields harbour the lowest number of plant species, and these together with the heavily grazed sizes are dominated by a high cover of *Galenia africana* (Aizoaceae). Lightly grazed sites have the highest structural complexity, with a high cover of succulents and non-succulent perennials. After the winter rains, annual plants occupy most of the bare ground in heavily grazed and previously cultivated sites. Seasonal changes in assemblages of ground-dwelling and flying invertebrates were determined by sampling during the four seasons at the same localities. Results of pitfall traps sampling for ground-dwelling invertebrates and coloured pan traps for flying invertebrates showed that overall species richness and diversity peaked in spring for flying invertebrates while peaks in richness for ground-dwelling invertebrates were in summer, with no difference in overall diversity. Overall abundance for ground-dwelling invertebrates was highest in summer and lowest in winter. Ground-dwelling invertebrate fauna was dominated by Formicidae and Araneae. Grazing and cultivation lead to skewed community composition of ground-dwelling invertebrates which favours disturbance tolerant and generalist species such as *Anoplolepis steingroeveri* (Forel). The lightly grazed areas favoured the specialised ant taxa and predators. Also, a trend for flying

invertebrates was that a high number of specialists and a high functional diversity occurred on the lightly grazed sites. Pollinator assemblages differed between seasons. In autumn and spring, the highest richness and abundances of pollinators were found in cultivated and heavily grazed sites. In summer, abundances of pollinators were highest in grazed sites and lowest on the cultivated fields. Flying invertebrate indicator species differ between seasons for each land use types, and these seasonal indicator assemblages are largely dependent on climatic factors while land use indicator assemblages are determined by vegetation structure and composition. Formicidae and Araneae are the only indicators for ground-dwelling invertebrate species. For conservation purposes, the results show that a large number of invertebrate species can be obtained by having a mosaic of different land use types, as these tend to have different seasonal assemblages for different taxa.

Opsomming

Die Sukkulente Karoo bioom se biodiversiteit word al hoe meer bedreig deur die ewig stygende druk vanaf menslike populasies en hul gepaardgaande grondgebruik tipes. Grondgebruik in dié area fokus hoofsaaklik op landbou, waar veebeweiding die dominante grondgebruik is. Gewasproduksie kom wel voor langs al die hoof aanhoudend vloeiende riviere, asook in sommige droër areas, maar laasgenoemde is grootliks afhanklik van reënval. Slegs sowat sewe persent van die bioom word amptelik beskerm, en selfs dié area ervaar wesenlike onderverteenwoordiging van Sukkulente Karoo biodiversiteit en neem ook nie sleutel ekologiese prosesse en biodiversiteit aandrywers in ag nie. Buite-reservaat bewarings inisiatiewe word dus dringend benodig, en die sukses van hierdie inisiatiewe sal afhang van 'n werklike begrip rondom ekosisteem funksie in die Sukkulente Karoo. Hierdie studie mik om die impakte van swaar beweiding, ligte beweiding en gewasproduksie (in 'n 30-jaar oue braakland) op versamelings van grondlewende en vlieënde ongewerweldes te bepaal. Seisoenale versameling veranderinge was ook bepaal. Plantegroei struktuur en samestelling was bepaal d.m.v. die lyn-onderskep metode. Hiermee kon bepaal word of patrone in plantegroei die patrone waargeneem in invertebraat versamelings verduidelik. Verlate velde huisves die laagste getal plant spesies, en word, soos die swaar beweide velde, gedomineer deur 'n hoë bedekking *Galenia africana* (Aizoaceae). Lig beweide liggings het die hoogste strukturele kompleksiteit gehad, met 'n hoë bedekking sukkulente asook nie-sukkulente meerjariges. Na winter reëns het eenjarige plante meeste van die kaal grond in swaar beweide velde en voorheen bewerkte velde beset. Seisoenale veranderinge in versamelings van grondlewende en vlieënde ongewerweldes was bepaal deur proefnemings oor al vier seisoene by dieselfde liggings. Resultate verkry van pitval strikke vir grondlewende ongewerweldes asook gekleurde pan strikke vir vlieënde ongewerweldes, wys dat algehele spesies rykheid en diversiteit vir vlieënde ongewerweldes 'n piek bereik in die lente, terwyl grondlewende ongewerwelde spesies rykheid eers piek in somer, met geen verskil in algehele diversiteit nie. Algehele volopheid van grondlewende ongewerweldes was die hoogste in somer en laagste in

winter. Grondlewende ongewerwelde fauna was gedomineer deur Formicidae en Araneae. Beweiding en gewasverbouing het gelei tot 'n skewe gemeenskapsamestelling van grondlewende ongewerweldes – wat steuring tolerante en algemene spesies soos *Anoplolepis steingroeveri* (Forel) bevoordeel. Die lig beweide areas bevoordeel gespesialiseerde mier taksons en predators. Ook vir vlieënde ongewerweldes was daar 'n hoë aantal spesialis spesies en hoë funksionele diversiteit op lig beweide velde. Bestuiwer versamelings het verskil tussen seisoene. In herfs en lente was die hoogste spesies rykheid en volopheid van bestuiwers gevind in bewerkte en swaar beweide liggings. In somer was volopheid van bestuiwers die hoogste in beweide liggings, en die laagste in bewerkte lande. Vlieënde ongewerwelde indikator spesies verskil tussen seisoene vir elke grondgebruik tipe, en hierdie seisoenale indikator spesies versamelings is grootliks afhanklik van klimaats faktore, terwyl grondgebruik indikator versamelings bepaal word deur plantegroei struktuur en samestelling. Formicidae en Araneae is die enigste indikators vir grondlewende ongewerwelde spesies. Vir bewarings doeleindes: resultate wys dat 'n groot aantal ongewerwelde spesies kan verkry word deur 'n mosaïek van verskillende grondgebruik tipes te hê. Hierdie mosaïek grondgebruik benadering neig om verskillende seisoenale versamelings vir verskillende taksons te huisves.

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CHAPTER 1. BACKGROUND

1.1 The Succulent Karoo

1.1.1 Geographical location

The Succulent Karoo is considered to be one of the earth's thirty four biodiversity hotspots (Mittermeier *et al*. 2004) and it is the world's only entirely arid hotspot (van Wyk & Smith 2001). This biome (Mucina *et al*. 2006) covers an area of approximately 80 809km^2 and forms part of the Karoo-Namib region (Hilton-Taylor & Le Roux 1989; Cowling & Pierce 1999). It is located along the western coastal strip along the Escarpment Mountains of southern Africa from the Lüderitz district of Namibia in the north and southwards to the Cape Fold Mountains, which marks the edge of the Cape Floristic Region (Hilton-Taylor 1994b). Most of the biome covers a flat to gently undulating plain with some hilly and broken veld, and an elevation mostly below 800 m, but reaching 1 500 m in the eastern part (Low & Rebelo 1996). According to Hilton-Taylor (1994a), the Succulent Karoo covers about 5.35% of the South African land surface. This makes the Succulent Karoo the fourth largest biome in southern Africa, after the Savanna, Nama-Karoo and Grassland biomes (Mucina *et al*. 2006).

1.1.2 Precipitation

The Succulent Karoo is limited to those areas with winter rainfall (Hoffman & Cowling 1987). The average annual rainfall is about 20-50mm in some areas (Desmet & Cowling 1999) and about sixty percent of this rain falls in winter (Milton *et al*. 1997; Cowling & Pierce 1999). Rains are usually reliable and predictable at any one location, not exceeding 250 mm over most of the region and with a very low coefficient of variation (Hoffman & Cowling 1987; van Wyk & Smith 2001). However, a high variation in timing and amount of rainfall is a common feature between parts of the biome (Hoffman & Cowling 1987) and this has profound influences on vegetation structure and function and has been implicated in the floristic diversity as well as plant life history strategies prevalent in the Succulent Karoo (Cowling & Hilton-Taylor 1999; Desmet & Cowling 1999). Average annual rainfall decreases westwards with the annual rainfall varying from 50 mm in the North-West to more than 400 mm in the Kamiesberg (an area situated in Namaqualand

and which lies above 1 200 m) (Hilton-Taylor 1994b; Milton *et al*. 1997; Venter *et al*. 1986). The high humidity at night and early morning and fog provide additional sources of moisture during the dry summer months (Milton *et al*. 1997). There is relatively high summer aridity and the duration of the growing season is short with cool temperatures (Milton *et al*. 1997; Ellery *et al*. 1991).

1.1.3 Soils

Arid environments are characterised by heterogeneous landscapes as a result of changes in soils and this has profound influence on plant species diversity in the area (Hilton-Taylor 1994b). Soil texture is of importance because it has a large effect on the ability of soil to retain moisture and withstand erosion (Ellis & Lambrechts 1986). The dominant soil types of the region are the red and yellow apedal soils with coarse sandy texture and with high base saturation (Ellis & Lambrechts 1986) and the shallow calcareous soils with texture ranging from sandy and loamy sand to sandy loam and sandy clay. Most of the soils of the area are very stony, mainly because of erosion of the top soil and subsequent weathering of the underlying shales (Hilton-Taylor 1994b). Due to lack of moisture in the arid regions, soil formation by weathering and leaching is very slow and large areas of bare rock may be present in most parts of the Succulent Karoo (Watkeys 1999). This has also resulted in weakly developed and shallow soils, which are base-rich to calcareous (Mucina *et al*. 2006).

Scattered across the landscape in the Succulent Karoo are mima-like mounds, locally known as heuweltjies, which have soils far richer in nutrients than the surrounding soils (Midgley & Hoffman 1991). Termites (Isoptera) have been found to play a major role in redistribution of nutrients in heuweltjies by collecting organic matter into the termitaria thereby liberating nutrients which would have otherwise been locked up (Midgley & Hoffman 1991; Palmer *et al*. 1999). These calcium-rich heuweltjies support vegetation which differs substantially from the surrounding vegetation (Midgley & Hoffman 1991).

1.1.4 Flora

Heterogeneity of soils (Cowling & Hilton-Taylor 1999) and the predictable cool season's precipitation that characterizes the Succulent Karoo are largely responsible for the floral composition of the biome (Cowling *et al*. 1994). The biome has exceptionally high numbers of plant species, belonging to such families as Mesembryanthemaceae, Crassulaceae and Euphorbiaceae (Cowling & Hilton-Taylor 1999; Hilton-Taylor 1994b). It is home to 6 356 plant species, 26% of which are endemic to the area and 14% are near endemic (Cowling *et al*. 1994; Jürgens *et al*. 1997). Typical species of dwarf shrub succulents are the members of Mesembryanthemaceae and these together with the succulent Asteraceae, Iridaceae and Hyacinthaceae are the biome's most distinctive features (Cowling & Hilton-Taylor 1999; Cowling & Pierce 1999). Geophytes comprise one of the largest floral components of the area and the annuals make up about eight per cent of the Succulent Karoo's flora (Hilton-Taylor 1994a; Cowling & Pierce 1999). Trees have the lowest contribution to floral composition and grasses are infrequent (Hilton-Taylor 1994b).

1.1.5 Invertebrate fauna

Although the Succulent Karoo is rich in plant and animal species (Vernon 1999), the distribution of many animals is poorly known, particularly among the invertebrate taxa (Hilton-Taylor & Le Roux 1989). The invertebrates are, however, the most dominant animals in the Succulent Karoo, especially the Hymenoptera, which have a special interrelationship with the flora (Vernon 1999) as the major contributors to the pollination system of the area (Mayer 2005). Some authors suggest that climate predictability has resulted in plant-pollinator specialisations (Colville *et al*. 2002) as a result of synchronised flowering and emergence patterns of pollinator species. The Coleoptera comprise the different beetles types, among them the monkey beetles (Scarabaeidae: Hopliini) which are important pollinators to species of annual Asteraceae and Mesembryanthemaceae (Picker & Midgley 1996). The high floral colour preferences (Colville *et al*. 2002) shown by these beetles suggest the most complex plant-pollinator interaction that has resulted in the floral success of the area (Johnson and Midgley 2001).

Other invertebrate taxa found in the Succulent Karoo are Gastropoda, Arachnida, Thysanura, Isoptera, Dermaptera, Hemiptera, Diptera, Lepidoptera, Hymenoptera: Apocrita, Orthoptera, Thysanoptera, Blattodea, Chilopoda, Collembola, Mantodea, Protura and Psocoptera (Dean & Griffin 1993; Dean & Milton 1993; Seymour & Dean 1999; Vernon 1999). There are very few Dermaptera, Thysanura, Hemiptera and Gastropoda species in the Succulent Karoo (Milton *et al*. 1992), while the Arachnida are one of the major groups of invertebrates found in the region, with high species richness and endemism in Namaqualand highlands (Vernon 1999). The butterfly and moth (Lepidoptera) fauna is poor despite the abundance of flowering plants, largely owing to the lack of water and larval foods during the dry summers (Whitehead *et al*. 1987). Isoptera are represented mostly by the small harvester termite *Microhodotermes viator* (Latreille), which is a dominant element of the termite fauna of the Succulent Karoo (Lovegrove & Siegfried 1989).

However, the rich biodiversity of the Succulent Karoo is threatened by human population pressures which pose several challenges to the future existence of this biome (Mucina *et al*. 2006). Land use practices such as grazing and cultivation have been identified as the major threats to biodiversity in the area (Dean & Milton 1995; Todd & Hoffman 1999; Mayer 2005). Although grazing is a form of land use that is compatible with biodiversity conservation, overgrazing has had major impacts on both plants (Todd & Hoffman 1999) and invertebrates (Dean & Milton 1995; Seymour & Dean 1999; Mayer 2005), and these grazing impacts cannot be separated from the land tenure systems in South Africa.

1.2 Land tenure systems
South Africa consists largely of grazing land (Hoffman & Ashwell 2001), especially in the more arid districts of the country where there is little water available either from rainfall or irrigation schemes for cultivation of crops. There are two main land tenure systems in South Africa, namely commercial and communal systems, with disturbance regimes and conservation status very dependent on land tenure (Esler *et al*. 1998). The commercial areas are those in which the land tenure system is freehold and where

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individuals have the right to buy and sell the land for profit. Land is privately owned and used for agriculture (extensive grazing, pastures and various crops) and, to a lesser extent, resort development (Esler *et al*. 1998). The communal areas are generally synonymous with the former homelands and self growing territories where individuals have few rights to own and sell the land (Hoffmann & Ashwell 2001). Due to different management systems in commercial and communal areas (Hoffman & Ashwell 2001), the communal areas have seen an increase in the stocking rates over the last decade while these have been kept close to the recommended number in the commercial farming areas (Todd & Hoffman 1999). The increase in the stocking rates in communal farms can be due to the fact that the livestock are kept for several reasons, like meat production, milk production, manure, draught power for ploughing and transport, ritual slaughter, bridal payments, and investment and cash sales (Hoffman & Ashwell 2001). As a result, vegetation condition is generally moderate to good in privately owned farms, while in the communally owned farms, vegetation is poor, with clear evidence of desertification (Esler *et al*. 1998).

1.3 Land use in the Succulent Karoo

1.3.1 Livestock farming

The Succulent Karoo has been used extensively for livestock farming (Allsopp 1999; Todd & Hoffman 1999) and the resultant problems of selective overgrazing, overstocking and trampling are therefore widespread (Hilton-Taylor & Le Roux 1989). The earliest evidence of livestock farming, a concept that was brought into the Succulent Karoo by the Khoikhoi dates back as far as 2 100 years ago. Livestock farming is still practiced to date, with the elder people of the area confined to areas such as the Richtersveld, Kamiesberg and Paulshoek which are known today as communal lands (Hoffmann & Ashwell 2001). The livestock farming that is practiced on the communal areas has resulted in severe overgrazing of the veld, due to high stocking rates and limited opportunities for herd rotation (Todd & Hoffman 1999). The commercial farms on the other hand are fenced, making it possible to practice some form of internal rotational grazing (Cowling & Pierce 1999). Hoffman *et al*. (1999) substantiate that in Paulshoek, communal farms have had increasing stocking rates for the past thirty years. This has resulted into clear cut differences between communal and commercial farms in terms of

both density of vegetation and dormant plant species (Seymour & Dean 1999). Resultantly there can be little doubt that high stocking densities in many communal areas have been a major cause of land degradation, especially by causing sheet and gully erosion. In some places land degradation has been so severe that it may prove irreversible (Hoffman & Ashwell 2001).

Land transformation through factors such as unsustainable livestock production has been one of the major concerns with regard to how it impacts on the flora in the Succulent Karoo and Succulent thicket biomes, as shown by Lechmere-Oertel *et al*., (2005), Seymour & Dean, (1999); Vohland *et al*., (2005); Todd and Hoffman, (1999). Several other studies such as Allsopp (1999); Mills & Fey (2004); Milne & Haynes, (2004); Beukes & Ellis (2003) have been centered on the effects of land use on soil properties. Studies by Bowie (1999); Todd & Hoffman (1999); Riginos & Hoffman (2003) and Cheney (2004) have focused on quantifying the differences in floral biodiversity and population dynamics in grazed areas (active and rested). Such studies have shown that although there are general decreases in shrub canopy cover, overall species richness generally remains unchanged as the loss of certain shrub species is compensated for by increase in species richness of non palatable shrub species such as *Galenia africana* L. (Aizoaceae) and other annual species. There is very little knowledge on what the cause of these vegetation changes is on the invertebrate assemblages.

1.3.2 Cultivation

Both intensive and extensive cultivation practices are the major threats to the biodiversity of the Succulent Karoo (Hilton-Taylor & Le Roux 1989). Large scale intensive cultivation of wheat, oats, rye and barley are some of the main agricultural activities on communal as well as commercial farms (Allsopp 1999). Areas that are intensely used for cultivation purposes and those which were used in the past are characterised by replacement of the perennial plant species and palatable perennials by annual plants that resprout normally after the winter rains (Dean & Milton 1995). The unpalatable and poisonous plant species are also common in these lands (Allsopp 1999). Where vegetation has been removed by cultivation, old fields take several years for the

vegetation to be restored or even fail to revert to natural vegetation for several decades (Allsopp 1999).The unpredictability of rainfall (Hilton-Taylor & Le Roux 1989) is one most common factor that leads to cultivated fields being abandoned and hence become fallow.

1.3.3 Mining

Mining, especially for diamond and heavy metals is also one of the land uses in the Succulent Karoo (Esler *et al*. 1998; Mucina *et al*. 2006). Mining activities result in wind erosion, creation of many access roads, tracks and borrows pits to service the mined areas and the processing of plants and slime dams magnify the direct effects of mining (Jackelman & Moll 1989).

Despite all these threats, only seven percent of the Succulent Karoo is protected as formal reserves (Myers *et al*. 2000). This area clearly underrepresents the diversity associated with the biome and does not incorporate key ecological processes and evolutionary biodiversity drivers (Mucina *et al*. 2006). Therefore, this study seeks to get a better understanding of the ecological processes driving the Succulent Karoo biome.

1.4 Thesis structure

As Vernon (1999) indicated, not much is known about invertebrates in the Succulent Karoo. Much paucity in knowledge about how these fundamental ecosystem function drivers are affected by land use still exists, and needs urgent attention. This study seeks to determine the responses of invertebrate assemblages to land use types, and in chapter 2, a detailed review of these responses will be explored. Chapter 3 and Chapter 4 present the experimental component of this research. Chapter 3 deals with the response of ground-dwelling invertebrate assemblages to heavy grazing, light grazing and cultivation while Chapter 4 deals with the response of flying invertebrate assemblages, with more emphasis on pollinators, to heavy grazing, light grazing and cultivation. Chapter 5 presents the general conclusions based on responses of both flying and ground-dwelling invertebrates to land use types and the recommendations for the conservation of invertebrates in the Succulent Karoo.

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CHAPTER 2. LITERATURE REVIEW

2.1 Introduction

Recently, there has been much concern with the long term changes in species composition, productivity, stability and usefulness of arid and semi-arid regions (Andrew 1988; Milton & Dean 1992; Podwojewski *et al*. 2002; Dodd 1994). Besides the extreme weather conditions that characterise arid and semi-arid regions (Dodd 1994), much focus has been on the role of livestock in changing the vegetation composition in these areas (Milton *et al*. 1994). Factors that influence these vegetation dynamics include intra- and inter-specific competition, herbivory and weather events (Yeaton & Esler 1990; Milton & Hoffman 1994) which lead to death of plant species and colonization by another species and spatial heterogeneity in vegetation (Yeaton & Esler 1990).

Conceptual models that explain vegetation changes and the resultant degradation in arid and semi-arid areas date as back as the early 1950s (Dodd 1994). These models include the state-and-transition model (Westoby *et al*. 1989), which Milton & Hoffman (1994) acknowledge being the best model that describes vegetation dynamics in arid and semi-arid rangelands, where influences of episodic events and grazing, as well as intrinsic vegetation change act intermittently. Westoby *et al*. (1989) also argue that the state-and-transition model can be put into practice by management. This model envisages that vegetation can be transformed to a variety of alternate states or communities of vegetation (Westoby *et al*. 1989) and the transitions between these states are triggered by factors such as fire, climatic change and intense grazing pressure,.

Grazing in communal areas in the Succulent Karoo is highly extensive and is mainly for subsistence (Hoffman & Ashwell 2001). Grazing disturbance by domestic livestock in southern African arid and semi-arid zones is now generally accepted as the source of significant vegetation change and degradation (Milton & Dean 1990; Todd 2000; Riginos & Hoffman 2003). Milton *et al*. (1994) described the step-wise process of grazing-associated degradation processes as defined by the state-and-transition model. The first step is the change in the age structure of plant populations (Roux & Vorster 1983; Milton

et al. 1994). Perennial plant species palatable to either domestic livestock (Gibson *et al*. 1992; Feber *et al*. 2001; Stewart 2001) or wild animals (Neff *et al*. 2007) produce fewer seeds and fewer surviving seedlings, and the age structure of plant population becomes dominated by older age plants due to trampling by livestock and foliage removal by animals that leads to decreased rates of seedling recruitment (Milton *et al*. 1994; Milton 1994). The second step is the decrease in plant diversity, size and growth and the associated decrease in secondary productivity. Plant species with their associated predators, facilitators and symbionts are lost (Milton *et al*. 1994). The third step is reduction in palatable perennial plant cover. Ephemeral and weedy species flourish after rains and compete with seedlings of palatable plant species. Perennials unpalatable to livestock become more abundant due a to higher recruitment potential (Milton & Dean 1990; Milton 1994; Milton *et al*. 1994; Todd & Hoffman 1999). In the last step, vegetation cover is lost, the vulnerability of soil to erosion is increased, soil becomes more saline and desertification sets in (Hoffman & Cowling 1990; Milton *et al*. 1994; Milton & Dean 1996; Allsopp 1999; Todd & Hoffman 1999). With all these changes, the associated changes in faunal composition are not inevitable.

2.2 Responses of flying invertebrates to grazing

As invertebrates also use the same plant resources as herbivorous animals, changes in composition and structure of plants are expected to have consequences on invertebrate assemblages either directly or indirectly (Morris 1990; Stewart 2001). Direct competition between the invertebrate herbivores and grazing animals for food sources is one common result (Jepson-Innes & Bock 1989). However, these changes in assemblages may differ depending on seasons (Jepson-Innes & Bock 1989) and species under study (Hutchinson & King 1980; Jepson-Innes & Bock 1989; Debano 2006). Indirect effects result from changes in plant species composition, for example, changes in habitats resulting from altered light intensity and alteration in oviposition sites and reduction in larval food sources (Feber *et al*. 2001; Stewart 2001; Neff *et al*. 2007). Impacts on invertebrates are detected by changes in community structure and population densities demonstrated by, for instance, invertebrate richness and diversity or changes in the whole species composition of areas of disturbance (Stewart 2001).

A series of studies on a wide range of invertebrates of grazed and ungrazed semi-arid chalk grasslands were conducted in England, Bedfordshire (Morris 1967; Morris 1968; Morris 1969). These together with studies in continental Europe (e.g. Gibson *et al*. 1992; Kruess & Tscharntke (2002) indicate that (1) livestock grazing can affect invertebrate communities through primarily changing vegetation characteristics such as composition, quality and architecture and (2) that invertebrates do not respond in a similar manner to livestock grazing; some groups are more sensitive to grazing than others. These results were consistent with those of Debano (2006) and Hutchinson & King (1980) in the United States and Australian grasslands respectively. Debano (2006) found a reduction in abundance of vegetation associated invertebrates in grazed lands compared to ungrazed lands. Beetles (Coleoptera) were more abundant, flies (Diptera) more diverse, while the Hymenoptera were both more abundant and diverse in the ungrazed areas. The Hemiptera were more diverse in the grazed areas. Hutchinson & King (1980) found a reduction in abundance and biomass of invertebrates with increased stocking rates of sheep. This reduction however was found to be progressive with increasing stocking level only for certain groups of invertebrates such as the Orthoptera.

In their adult stage, most of the flying invertebrates are pollinators to the vast array of plants in the Succulent Karoo (Struck 1994). Grazing can affect pollinating insects by altering the availability of nesting sites and water resources while trampling by livestock can directly destroy habitats of ground nesting bees (Hymenoptera) and wasps (Hymenoptera) (Mayer 2004). A high abundance and diversity of bees were found by Mayer (2004) in moderately grazed sites in Paulshoek, as opposed to the heavily grazed sites. The same results were also obtained by Robertson & Van Noort (2003) in the Eastern Cape, South Africa; Bees and aculeate wasps (Hymenoptera) which are also known to form the major group of entomophilous insects in the Succulent Karoo (Struck 1994) were found to have higher species richness in intact thicket where browsing was mainly by game. The neighbouring fence-line contrasted sites where browsing by goats was very high, had low species richness of bees and aculeate wasps.

The monkey beetles (Coleoptera: Scarabaeidae: Hopliini) which are also known to be an important group of cantharophilous insects in the Succulent Karoo (Colville *et al*. 2002; Goldblatt *et al*. 1998; Picker & Midgley 1996; Struck 1994), have been shown to respond to grazing pressures. Colville *et al*. (2002) found a shift away from perennial and bulb pollinator guilds of monkey beetles towards those favouring weedy annuals in grazed sites. Monkey beetles abundance, diversity and richness showed consistently higher trends in undisturbed sites unlike in disturbed sites. Picker & Midgley (1994) also showed a very close association of one scarabeid species; *Hoplocnemis crassipes* (Oliver) (Coleoptera: Scarabaeidae) with the roots of *Eriocephalus ericoides* (Asterales: Asteraceae) one of the dominant shrubs in a field of disturbed renosterveld. Association of scarabaeid larvae with roots of plants was also studied by Ogawa & Mitamura (1981). Scarabaeid larvae were found to be most abundant in the top 5cm layer of the soil, where most roots occur in grazed pastures. In pastures where grazing was excluded, the abundance decreased in the top soil, where proportion of roots was also found to be less. In Australia, Roberts & Morton (1985) found that grazing pressure increased the biomass of certain scarabaeid larvae, but this increase was only up to a certain stocking level. The present study is therefore expected to show differences in responses of different species of scarabaeids, as one example of the flying invertebrates and an important pollinator group (Picker & Midgley 1996), with the different levels of grazing and cultivation. The latter could be regarded as the extreme level of land-use in which vegetation has shifted to predominance by *Galenia africana* L. (Caryophyllales: Aizoaceae) and *Hermannia amoena* (Dinter) (Malvales: Sterculiaceae) as the only dominant shrubs during dry periods and the upcoming of annuals during the wet winter-spring periods.

2.3 Responses of ground-dwelling invertebrates to grazing

The reduced amounts of herbage, surface litter and surface pore space that accompany heavy grazing affect particularly the abundance of soil and ground-dwelling invertebrate species (King & Hutchinson 1976; Hutchinson & King 1980; Stewart 2001). Soil compaction can also increase pH through poor aeration and this may contribute to reduced abundance of soil invertebrates (King & Hutchinson 1976).

In arid shrublands, grazing leads to nutrient impoverishment and this together with soil compaction through trampling reduces the plant biomass (Andrew 1988; Milton & Dean 1992) and leads to a reduction of palatable plant species (Podwojewski *et al*. 2002) and an increase in short-lived plant species at the expense of deep-rooted perennials (Andrew 1988; Milton & Dean 1992) coupled with an increase in species resistant to trampling (Rambo & Faeth 1999). The density and biomass of root-feeding invertebrates such as the Scarabaeidae larvae (Hutchinson & King 1980; Roberts & Morton 1985) and the cicadas (Hemiptera: Cicadidae) (Milton & Dean 1992) are also affected by these changes. A study in Karoo shrubland, South Africa (Milton & Dean 1992) showed that populations of long-lived Cicadidae declined on heavily grazed, degraded sites as opposed to moderately grazed and stock exclosures. Densities of Cicadidae were positively correlated with the cover of long-lived perennials which were predominant in the moderately grazed sites and exclosures and negatively correlated with the cover of short-lived plants, which increased as range quality decreased.

In woodlands and grasslands of Australia, grazing by cattle has been associated with reduced vegetation, which in turn changes the amount of litter and microclimate (Henderson & Keith 2002; Yates *et al*. 2000). Under heavy grazing, these changes have been attributed to changes in invertebrate assemblage structures (Bromham *et al*. 1999). Regardless of the level of grazing, Harris *et al*. (2003) demonstrated that grazing intensities can change the patchiness of the understorey vegetation, influencing the ground-dwelling spider (Araneae) assemblage.

2.4 Responses of flying invertebrates to cultivation

In many parts of the globe, land-use activities continue to influence ecosystem patterns and processes (Foster *et al.* 2003) and the Succulent Karoo is not an exception, regarding the history of cultivation in the area (Dean & Milton 1995). Most of the arable soil in the arid Karoo has been ploughed in the past, and undisturbed soils are difficult to find, with the alluvium being conspicuously characterized by low plant cover during dry periods, dominance by a few succulents and prevalence of alien plants (Dean & Milton 1995). Cultivation and the associated vegetation and environmental changes, affect invertebrates

at all trophic levels (Foster *et al.* 2003; Purvis & Curry 1984). Microbial populations of soil fauna are altered and the invasion of exotic invertebrates such as earthworms, is often facilitated (Callaham *et al*. 2006).

Plowing homogenizes the upper soil horizons, leaving a uniform, upper horizon that may be depleted of carbon and nitrogen, although specific impacts vary with cropping type, duration and application of fertilizers (Siemann 1998). When farmed sites are abandoned, physical and biological soil development proceeds slowly (Foster *et al*. 2003). Effects of agricultural soil changes, by for instance, liming and fertilization on invertebrates are inconsistent and depend on the invertebrate trophic levels (Siemann 1998; Purvis & Curry 1984). The results of a study by Siemann (1998), in which only trophic levels of vegetation associated arthropods (herbivores, detritivores, predators and parasites) were studied, showed that long term fertilization lowered plant species richness which in turn significantly increased the species richness of parasites and predators and lowered the richness of herbivores and detritivores. If agricultural fields are abandoned, they experience changes in organic carbon and total soil nitrogen content during recovery (Foster *et al*. 2003), and the associated changes in vegetation. Dean & Milton (1995) found that succession in fallow fields in the Succulent Karoo resulted in changes in plant composition across the old fields.

Robertson & van Noort (2003) looked at diversity of wasps and bees (Hymenoptera) across a mosaic of transformed agricultural lands on Bokkeveld Plateau, South Africa. They found fallow lands and wheat fields to have the highest numbers of species of Ichneumonidae. They attributed this to the fact that some of these Ichneumonidae might be parasitoids on wheat pests and herbivorous insects feeding on geophytes growing in or around the fields. Apoidea species were found to be fairly similar across land uses, and this they attributed to constraints in sampling procedures.

2.5 Responses of ground-dwelling invertebrates to cultivation

In arid and semi-arid regions, livestock production and cereal cultivation are usually depicted as major causes of land degradation and desertification (Macdonald 1989). In the Karoo, most of the soils are too shallow to be ploughed (Ellis & Lambrechts 1986) or too distant from water sources for irrigation (Dean & Milton 1995). However, Macdonald (1989) estimated that in the Karoo agricultural region, about 16% of the area cultivated is being unwisely cultivated under dry-land conditions. This resulted in considerable areas in the Karoo where cultivation was practiced in the historic past (Dean & Milton 1995) and which are no more cultivated. The vegetation in these areas fail to revert to natural vegetation for several decades indicating that soil processes may have been disrupted (Allsopp 1999).

Plant diversity and cover, litter and dead wood influence microclimate and food availability for ground-dwelling invertebrates (Andersen 1997), thereby structuring and changing their assemblages both directly and indirectly through competition. A study by Dean & Milton (1995) in the southern Karoo showed that the cultivation of river terraces and alluvial soils causes long-term changes in plant and invertebrate communities. They discovered that succession on the old fields is slow and this was accompanied by changes in trends from generalists to specialists in ants (Hymenoptera: Formicidae) and beetles (Coleoptera).

Seasonal changes in ssemblages are also common. Dean (1992) views some of the seasonal differences as determined by temperature. In a study by Netshilaphala *et al.* (2005) in the Succulent Karoo, assemblages of ants were not only determined by mining disturbance but they also differed between seasons. The generalists such as *Anoplolepis steingroeveri (Forel) (Hymenoptera: Formicidae)* were found to be significantly abundant in autumn than in winter.

The changes in assemblages of spiders (Araneae: Ammoxenidae) which are predatory were attributed, among other factors by Dean & Milton (1995) to soil texture. As has been determined by Allsopp (1999) cultivation resulted in changes in soil patterns and

processes in the Succulent Karoo. The cultivated areas are therefore expected, as a result of factors such as vegetation changes (Dean & Milton 1995) and changes in soil properties (Allsopp 1999; Foster *et al.* 2003) to have different composition of ground-dwelling invertebrates and these assemblages are also expected to differ seasonally (Netshilaphala *et al.* 2005).

2.6 Indicator taxa

Invertebrates form an integral part of ecosystems and occur at all levels of the food web (Seymour & Dean 1999). They play important roles in ecosystems as pollinators of flowering plants, recycling of soil nutrients by decomposing organic matter and hence the alteration of structure and fertility of soil (Blondel & Aronson 1995; Rivers-Moore & Samways 1994). In agriculture, invertebrates, especially insects, perform important roles as pests, controllers of pests, prey and predators, and are major contributors to biodiversity and general indicators of ecosystem health (Holland *et al*. 2005). Studies examining the responses of invertebrates to land use in the Succulent Karoo (Mayer 2005; Mayer 2004; Seymour & Dean 1999; Milton & Dean 1992) suggest that invertebrates can be sensitive to grazing intensity. Although varying in their responses to disturbance, invertebrates are generally considered as good indicators of landscape change as they are abundant, widespread and species rich (Samways 1994). Because many species exhibit populations with short generations that are sensitive to environmental fluctuations, they have greater potential for close tracking of environmental variations than do populations of larger animals and for these reasons are generally considered as good indicators (Belovsky & Slade 1995).

Indicator taxa are species or higher taxonomic groups that can be used to measure, monitor or indicate some aspect of change in ecosystem conditions, either by changes on their density, abundance or loss from local scenarios (New 2000; Hilty & Merenlender 2000). For example, indicator taxa have been used to evaluate ecosystem health (Hilty & Merenlender 2000), using either single species, higher taxa or assemblages (Büchs *et al*. 2003; Scott *et al.* 2006; Roberge & Angelstam 2006). They can be used to reflect environmental quality and in many instances provide good bases for monitoring the

changes that occur as habitats are degraded or restored as conservation management is implemented. Several criteria for selecting indicator groups and definitions of various forms together with combinations of different groups to constitute indicator taxa sets have been developed (McGeoch 1998; New 2000; Duelli & Obrist 2003). The most accurate indicators of biodiversity are proven linear correlates of the entity or aspect of biodiversity being evaluated (Duelli & Obrist 2003).

Caughley & Gunn (1996) maintain that bioindication is a subdiscipline of conservation biology, and its primary goal is therefore, the application of scientific knowledge to the management of ecological relationships between species and their distribution and abundances. On the one hand, knowledge at species level is always not available, especially for invertebrates and the use of Rapid Biodiversity Assessment (RBA) to determine taxa to morphospecies level have recently been adopted (Oliver and Beattie 1996). This lack of knowledge that necessitates the use of morphospecies requires care consideration in choosing morphospecies as indicators. The selection of indicators using the method of Dufrene & Legendre (1997) suffices well in this regard (McGeoch & Chown 1998). This method calculates an indicator value (IndVal) of a species expressed as a percentage. This value would be highest if a species is both unique to the site (high specificity), as well as being abundant and widespread in that site (high fidelity). Thus species with high specificity and fidelity to a site would have high probability of being sampled during the monitoring and assessment. One of the advantages of using this method of indicator selection is that if species show similar specificity and fidelity to certain sites, it implies that those groups of sites have the highest probability of encompassing a viable probability of such species. Thus in that situation, such sites can be identified as core conservation areas for the species identified. This is particularly important where little to no distributional or biological information is available for such species (McGeoch & Chown 1998). Thus in the present study, the Dufrene & Legendre (1997) method of indicator selection was used because of its ability to be used with morphospecies.

2.7 Aim of the study

The main aim of this study is to provide fundamental understanding of how different land use types, namely grazing and cultivation, can impact on diversity and abundance of invertebrate assemblages, concentrating mainly on seasonal differences. Invertebrates areknown to show seasonal changes in their assemblages. Seasonal differences observed in the study could be used, for instance, to determine the best sampling season for the different taxa in future monitoring studies.

2.7.1 Objectives of the study

The aim is much generalized and can be broken down into the following objectives:

➢ To establish how different land use types affect the abundance and diversity of both the ground dwelling invertebrates and flying invertebrates across seasons.

➢ To determine the vegetation cover and composition for the areas of different land uses across seasons.

➢ To determine ground dwelling and flying indicator species for land use across seasons.

➢ To provide management recommendations that would best conserve invertebrate fauna in the Succulent Karoo.

2.7.2 Key questions

To reach the overall aim and above objectives, this study aims to answer the following key questions:

▪ Is there any difference in terms of abundance, composition, richness, evenness and diversity of both ground dwelling invertebrates and flying invertebrates across land use types and seasons? Here, an emphasis within flying invertebrates was put on pollinator taxa, as these play a major role in ecosystem function, as well as the different feeding guilds which are expected to differ with land use type.

▪ Are there certain groups of invertebrates that suddenly change as a result of land use and can therefore be regarded as indicators for land use during the four seasons?

- Do the observed vegetation and weather changes explain changes in invertebrate assemblages across land use types and seasons?
- Are there any implications of the findings to the conservation of invertebrates in the Succulent Karoo?

2.8 Predictions

The quantity, quality and heterogeneity of resource base should affect the diversity of consumers. Plant productivity, composition and diversity may influence the diversity of invertebrate trophic groups (Siemann 1998). According to the resource rarity hypothesis, plant productivity may increase the diversity of herbivorous invertebrate taxa by increasing the rare resources (Siemann 1998). Increasing the herbivore diversity could also increase diversity of predators and parasites, though these may also be directly be affected by increased plant productivity. Following this hypothesis, the lightly grazed sites are expected to have higher plant species richness, which would provide rare resources for a variety of invertebrate taxa, thus increasing their richness and abundance, for both ground-dwelling and flying taxa. In the same way, vegetation patterns in the Succulent Karoo are known to depend on rainfall and follow a seasonal pattern, with the annual plant diversity increasing in degraded areas after the winter rainfall and flowering during the winter-spring seasons (Esler 1999). These vegetation changes in heavily degraded areas are expected to lead to a bottom-up effect, in which diversity of species that depend on annual plants increasing during the winter and spring seasons.

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CHAPTER 3. RESPONSES OF THE GROUND-DWELLING INVERTEBRATES TO DIFFERENT GRAZING INTENSITIES AND CULTIVATION IN A THIRTY YEAR OLD FALLOW FIELD, IN THE SUCCULENT KAROO.

3.1 Introduction

Invertebrates are found in all habitats and dominate the diversity of species, making up approximately 90% of all species (Duelli *et al*. 1999; Pimentel *et al*. 1992). However, disturbances of habitats whether by physical or biological factors can affect species richness and abundance of the ground-dwelling insect communities (Ríos-Casanova *et al*. 2006). Physical habitat disturbances have been attributed to many factors such as uncontrolled grazing and the deterioration of agricultural lands (Pimentel *et al*. 1992). However, there has been much of debate recently on whether land use practices such as grazing give rise to environmental degradation or such changes can be attributed to abiotic factors such as climatic regimes (Dodd 1994; Brown & McDonald 1995). Arid and semi-arid environments have harsh environmental conditions which are characterised by frequent incidences of high solar radiation, wide fluctuations of temperature, and low precipitation regimes (Ríos-Casanova *et al*. 2006). The extreme climatic conditions make it difficult to distinguish the grazing and cultivation impacts from the climatic impacts in these systems but studies like Dodd (1994) have managed to give a clear cut separation between grazing and climatic impacts, by a detailed review of literature cited before the 1960's till the late 1980's, and delineating which paradigms best describe the shift in vegetation properties in response to grazing and climatic factors in arid areas.

In agricultural landscapes, Carabid beetles (Coleoptera: Carabidae) and other ground-dwelling invertebrates (Purvis & Curry 1984) were found to display different diversity and abundance levels depending on their trophic level in response to application of farmyard manure and weeds. The relationship of ant diversity and mining activities (Netshilaphala *et al*. 2005), vegetation and soil factors (Ríos-Casanova *et al*. 2006) and grazing (Sassi *et al*. 2006) have shown drastic responses of ants as ground-dwelling invertebrates to land use. Studies on termites (Milton *et al*. 1999; Coaton 1948; Coaton & Sheasby 1975) have indicated association of termites with overgrazed lands. In the

Succulent Karoo, a study by Dean & Milton (1995) on fallow fields revealed that succession in such fields is apparently slow, with the ground-dwelling invertebrate assemblages responding differently to age of the field. Seymour & Dean (1999) found grazing to affect abundances of ground-dwelling invertebrates and such effects were associated with changes in vegetation cover in grazed sites. All these are attributed to the fact that invertebrates have the ability to rapidly respond to environmental changes because of their short life cycles and specific habitat needs.

Invertebrates also have the ability to respond to climatic conditions such as rainfall, humidity, wind speed, day length and sunlight (Retana & Cerdá 2000; Pinheiro *et al*. 2002; Lindsley & Skinner 2001; Netshilaphala *et al*. 2005). The Succulent Karoo experiences extreme seasonal fluctuations in temperature and rainfall (Dodd 1994; Brown & McDonald 1995) and these changes are usually reflected by invertebrate assemblages (Sassi *et al*. 2006; Netshilaphala *et al*. 2005). The aim of this study was therefore to quantify seasonal and land use changes in ground-dwelling invertebrates in the Succulent Karoo by addressing the following questions:

1. Is there any difference in terms of abundance, species richness, diversity and evenness of ground-dwelling invertebrates in the three land use types across seasons and within seasons? The three land uses being light grazing in commercial farms, heavy grazing in communal areas and cultivation of fodder crops in a 30 year fallow field.

2. Do the observed weather and vegetation/habitat changes explain changes in ground-dwelling invertebrate assemblages across land use types and seasons?

3. Are there groups of ground dwelling invertebrates that can be regarded as indicators for land use during the four seasons?

4. Are there any implications of the findings to the conservation of ground-dwelling invertebrates in the Succulent Karoo?

3.2 Material and methods

3.2.1 Study area and sampling design

This study was conducted in Paulshoek (30º20′S; 18º14′E), one of the six communal villages in the Leliefontein rural district of Namaqualand, Northern Cape Province (Todd & Hoffman 1999; Simons 2005). Leliefontein is located in the Kamiesberg, an escarpment about 50 km wide between the low-lying Sandveld in the west and the Bushmanland plateau in the east (Todd and Hoffman 1999). The area is part of Namaqualand, a winter-rainfall desert of about 50 000 km^2, characterised by a number of unique biological features (Cowling *et al.* 1999). The climate of the area is characterised by winter rainfall estimated at 200 mm per annum with a co-efficient of variation of 33% (Todd & Hoffman 1999). Extremes in temperatures and humidity result in large annual and daily temperature fluctuations (Desmet & Cowling 1999).

The Succulent Karoo vegetation of the area includes members of the families Aizoaceae, Asteraceae, Liliaceae, Crassulaceae, Geraniaceae, Asclepidaceae and Euphorbiaceae (Cowling & Hilton-Taylor 1999). The leaf succulents mostly dominate the sandy plains and the non-succulent shrubs dominate the rocky hills with trees and grasses not forming an important component of the vegetation (Todd & Hoffman 1999). Evergreen and deciduous shrubs up to 1 m tall and a diverse annual and geophyte flora which follow the winter rains are typical of the area (Allsopp 1999). The abundance of most of the palatable shrub species decrease greatly under grazing as a result of selective grazing by livestock resulting in a shift to assemblages dominated by toxic woody plants such as *Galenia africana* L. (Aizoaceae) (Milton & Hoffman 1994). Where non-palatable plants are common, increased grazing pressure has been observed to result in a shift from perennial to annual vegetation (Milton *et al.* 1994). The grazing pressure in the communal areas in Paulshoek has been high with stocking rates twice that recommended for the region by the South African Department of Agriculture (approximately 6 ha per small stock unit) while the private farms maintain lower stocking rates (12 ha per small stocking unit) (Todd & Hoffman 1999). The grazing regime of Paulshoek can be characterised as being heavily and continuously grazed while the neighbouring commercial farms such as Remhoogte and Witwater are moderately and rotationally

grazed (Todd & Hoffman 1999). This gave rise to marked fence-line contrasts between communal and commercial farms. In the Paulshoek area, cultivation of fodder crops such as wheat and barley is occasionally practiced depending on rainfall regimes and availability of resources. Farmers do not use commercial fertilizers on their fields and they rarely use animal manure from kraals (Allsopp 1999). Due to the tenure system associated with the cultivated land, the fields may remain fallow for several years provided families with rights to those lands choose not to cultivate them (Allsopp 1999).

Two localities, namely Kleinfontein and Kuile each adjacent to a commercial and privately owned farm; Witwater and Remhoogte respectively were selected for comparative studies of impacts of grazing on invertebrates. The continuously high stocking rates on communal rangelands in Kuile and Kleinfontein resulted in clear fence line contrast between these communal rangelands and their neighbouring commercial farms. In Kleinfontein, a stretch of a 30 year old fallow field (Gert Joseph pers. comm.) was also sampled. For simplicity, this fallow field is referred to as a cultivated field. This *Galenia africana*-dominated field is characterised by resprouting of annuals after the winter rains. Figure 3.1 shows the map of the study area, indicating the position of the study plots. Figures 3.2A, 3.2B and 3.2C respectively show photographs of the fence-line contrast between the grazed sites in Kleinfontein, Kuile and the cultivated field (30 years fallow).

Two heavily grazed plots and two lightly grazed plots were selected at the Kuile communal site and commercial site (Remhoogte), respectively. The third plots for the heavily grazed and lightly grazed sites were located at the Kleinfontein communal and commercial (Witwater) site, respectively. All the three plots for the cultivated field were located in Kleinfontein. The areas where differences in aspect, rockiness and slope were obvious were avoided in choosing the study plots. Within each plot, three grids were chosen, approximately 150 m apart. In Kuile, grids were made at least 1 km from the fence, but this could not be achieved in Kleinfontein due to topographic constraints. The cultivated field was found in Kleinfontein only and because there were no neighbouring fallow fields, all the plots had to be at this single location. This possibly resulted in

pseudoreplication. However, a 150 m distance between sampling grids was maintained to avoid spill over effects (Seymour & Dean 1999). A similar distance was maintained between the fence and the sampling grids at the heavily grazed and lightly grazed sites in Kleinfontein. No pristine plots were investigated to determine which land use type has the least impact because there are no pristine areas under conservation located in this area, therefore such comparison was not possible.

It is acknowledged that due to time constraints and limited resources, the number of replicates were low; for land use types (n = 3) and than for seasonal changes, the sample size was actually 1. The results obtained could therefore be less conclusive due to this low replication. The cross-array of pitfalls used in this study to sample ground-dwelling invertebrates was previously used by Boonzaaier (2006) in the Cape Floristic Region. The author found that at local site scale, increases in sampling effort in terms of increasing the sampling duration (from one to five days to six to ten days) and sampling intensity (number of sampling units in an extent) resulted in a similar increase in ant species richness captured. McGeoch *et al*. (2002) also acknowledge that due to time constrains and limited resources, comparative studies are often obtained using a single sampling period and trapping method.
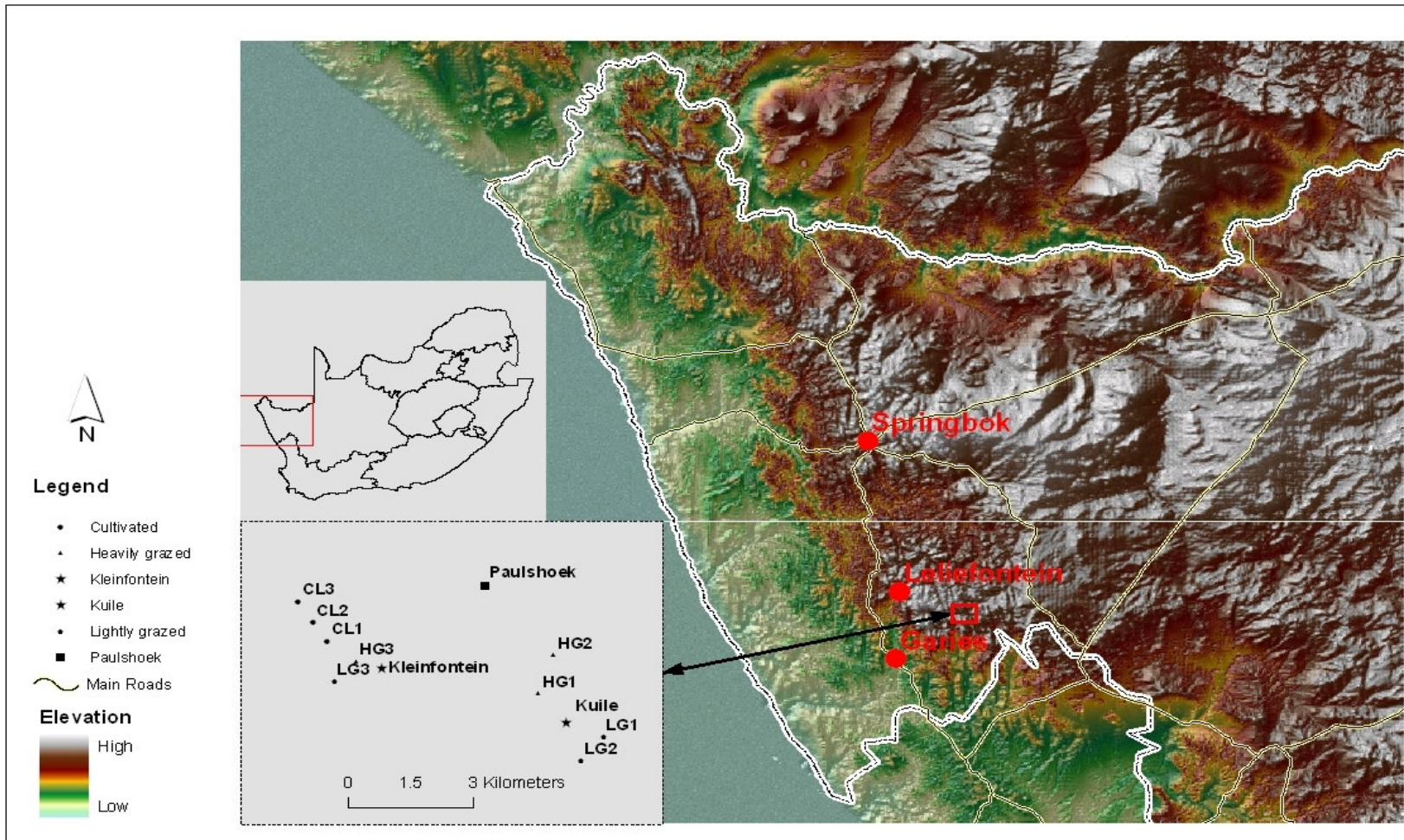
Figure 3.1: Map showing study plots at Paulshoek, Northern Cape, South Africa.

Figure 3.2A: Fence line contrast between the heavily grazed sites and lightly grazed sites in Kleinfontein

Figure 3.2B: A fence-line contrast at Kuile in Paulshoek, showing the heavily grazed and lightly grazed sites.

Figure 3.2C: A 30 year old fallow field at Kleinfontein dominated by a perennial shrub, *Galenia africana* L. (Aizoaceae).

The first sampling was conducted in March 2006 for the autumn season. The second sampling was conducted in July 2006 in the winter season. Spring and summer samplings were conducted in September 2006 and January 2007, respectively. The position of each grid was marked with a Garmin GPS during the first sampling, so that the same grid was used during subsequent samplings.

Thus, the three treatments (land use types) were investigated, with the following abbreviations that indicate the land use types:

- LG: The lightly grazed sites in commercial farm of Witwater and the lightly grazed sites in commercial farm of Remhoogte.
- HG: The heavily grazed sites in communal rangelands of Kleinfontein and the heavily grazed sites in communal rangelands of Kuile.
- CL: The 30 year fallow field in Kleinfontein, referred throughout as cultivated sites.

Pitfall traps were used to capture the ground-dwelling invertebrates. Pitfall traps are effective in sampling ground-dwelling invertebrates in open areas (New 1999; Read & Andersen 2000; Harris *et al*. 2003). The traps consisted of plastic containers of about 6.5 cm depth and 4.5 cm diameter. A cross array of nine pitfall traps (Perner & Schueler 2004), two on each arm of the cross were laid in each of the grids and one in the centre (Figure 3.3). The grid was square shaped and covered an area of 40 m by 40 m. The traps were 10 m apart, and were sunk level with the surface of the soil and about three quarters filled with water and a few drops of liquid detergent were added to break the surface tension (Seymour & Dean 1999).
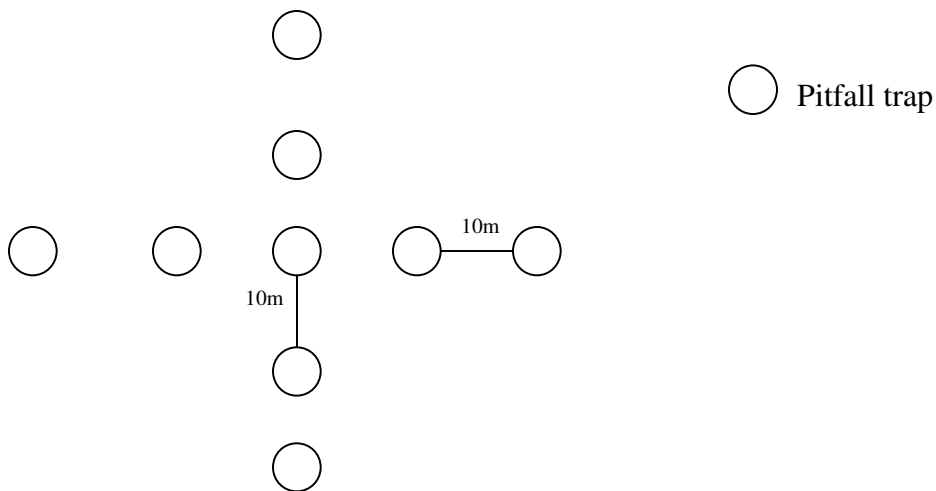
Figure 3.3: Layout of pitfall traps per sampling grid.

The contents of the traps were collected after seven days by removing the traps from the ground. Specimens were removed from the traps with narrow-tipped featherweight forceps and put in plastic sample bottles in which 70% ethyl alcohol was added and marked according to sampling date and site. These featherweight forceps were used as they are very pliable and do not crush even very fragile specimens. This procedure was repeated for each sampling season. Thus, sampling consisted of a total of 243 pitfalls in 27 sampling grids, nine grids for each of the land use types for a seven-day period each sampling season. Since sampling for ground-dwelling invertebrates was done together

with the flying invertebrates (see chapter 4), grids in Kuile were sampled for the first seven days and in the following seven days, grids in Kleinfontein were then sampled. This was due to the large number of specimens collected during sampling. It was thus not be feasible to sample both Kuile and Kleinfontein simultaneously.

The invertebrates were then sorted and counted in the laboratory under a dissecting microscope and identified into Recognisable Taxonomic Units (RTUs) based on their morphological similarities (Rees 1983). Estimates of diversity and richness obtained by using RTUs have been found to be comparable to those obtained by taxonomists (Oliver & Beattie 1996a; Oliver & Beattie 1997). RTUs were then identified to the lowest taxonomic level by specialists at Centre for Invasion Biology (CIB) at the University of Stellenbosch and professor Henk Geertsema, from the Department of Conservation Ecology and Entomology, University of Stellenbosch (see acknowledgements). Voucher specimens are kept at the Entomology Museum, University of Stellenbosch, South Africa.

3.2.2 Vegetation sampling and weather data

For each of the sampling events, vegetation structure next to each of the pitfall grids was sampled. Vegetation surveys were carried out to determine if changes in structure and composition explain the assemblages of ground-dwelling invertebrates in the three land use types. Rock cover, bare area and plant species composition and height were recorded along a 50 m line close to the pitfall cross using the line intercept method (Milton & Dean 1992) to estimate their cover (Colville *et al*. 2002). For each of the grids, a 50 m transect was sampled once during the seven-day sampling period for every season. At every 1 m intercept along the transect, the heights of plant species that were directly hit by the measuring tape were determined using a 5 m measuring tape. Herbarium specimens and pictures were taken for identification for plant species that could not be identified in the field. A Sony Cyber-Shot camera with 7.2 Megapixel, 3X optical Zoom lens and Carl Zeiss lens was used to take pictures. Plants were later identified at least to genus level. Growth and life form were also determined. Identification was done by Professor M.T. Hoffman, Lesley Hill Institute of Plant Conservation, University of Cape

Town. Bare ground as well as rocky areas were noted along the transect. These were also hits at the 1 m intercept along the transect. This enabled the estimation of the total percentage cover, percentage cover of each plant species and cover of exposed and rocky area as hits for each category divided by the transect length and multiplied by one hundred. Plants were classified as grasses, annuals, succulent perennials and non-succulent perennials, as determined from life form and growth form. Vegetation structure was estimated by assigning different height classes to all perennials: succulent perennials greater than 25 cm, succulent perennials less than 25 cm, non-succulent perennials greater than 25 cm and non-succulent perennials less than 25 cm (Todd & Hoffman 1999). Cover for the different vegetation classes, annuals, grasses, rocks and bare ground were then estimated.

Weather data for the area were obtained from BIOTA web site (www.biota-africa.org). The weather station is situated at the fence between the BIOTA observatories Leliefontein 624 (Paulshoek) and Remhoogte 416 (Rooiwal) (30º 23' 41.1 ''S, 18º 17' 10.1''E). The weather data included rainfall, minimum and maximum temperatures, relative humidity of the air and minimum and maximum wind speed for the seven-day sampling periods for every season.

3.2.3 Data analyses

For vegetation sampling, mean (±SD) percentage cover for each of the categories; annuals, bare area, grass, rocks, succulent perennials and non succulent perennials were determined using grid data for each of the land uses for each season. For height classes, mean (±SD) were determined. Statistical differences were determined using Mann-Whitney U-test. Mean (±SD) number of plant species was also determined for each land use type for all seasons. Statistical differences were determined using one way ANOVA for each season. The two plant species that had the highest percentage cover per land use were also determined. This was calculated as the mean number of hits at 1 m intercept along the transect, divided by the transect length and multiplied by 100. These were averaged over all the sites in each land use type. These were determined for all the seasons.

Weather data were plotted to depict their variations. Rainfall was plotted for the year in which sampling was conducted (March 2006 to January 2007). Mean (±SD) for minimum air temperature, wind speed, relative humidity of the air and solar radiation were plotted for the seven-day seasonal sampling.

The pitfall data were pooled into a single sample per sampling point, giving a total of n = 9 plots, three for each of the land use types. Only taxa which were regarded as ground-dwelling were used (Uys & Urban 1998). Total abundance, diversity, species richness and species evenness of invertebrates were determined across seasons for all invertebrates combined. Diversity was calculated using Shannon-Wiener diversity index (H) which also takes into account evenness of species abundances. These were calculated using CanoDraw in CANOCO, version 4.5 (Lepš & Šmilauer 2003). Results were tested using factorial ANOVA with season and land use as the main effects and Bonferroni tests as post-hoc test in STATISTICA 7 (StatSoft Inc. 2003). Relative abundances were calculated across seasons for each ground-dwelling invertebrate orders and for invertebrate orders within seasons and between land use types. The relative abundances of ants (Hymenoptera: Formicidae) were calculated separately from the other taxa, as their abundances were far more than those of other taxa, and could lead to masked results. This was done for both seasonal differences and land use type. Thus for Formicidae, relative abundances were determined for the different genera and species. Species richness was determined for ground-dwelling invertebrate orders across seasons and within seasons between land use types for taxa (orders and families). Relative abundance is the absolute number of individuals of a species at each plot divided by the total number of individuals of all species at that plot multiplied by one hundred Statistical differences were determined with Kruskal-Wallis ANOVA, using Mann-Whitney U-tests as post hoc tests, as data were not normally distributed.

To determine which species were characteristic of land use, their indicator values were determined using the Indicator Value Method by Dufrêne and Legendre (1997). This method determines the indicator value (percentage INDVAL) for each species, looking at

both uniqueness of a species to a habitat (specificity) and its frequency of occurrence within that habitat (fidelity) (Dufrêne and Legendre 1997; McGeoch *et al*. 2002). A value of 70% was regarded as benchmark, with species having significant values greater than this benchmark regarded as indicators for land use (Botes *et al*. 2006; McGeoch *et al*. 2002).

Multivariate ordination techniques were used to determine patterns in species space relative to land use. Data sets were first reduced by eliminating species whose abundance was less than 5 individuals in all (Seymour & Dean 1999; Gaston 1994). Redundancy analysis (RDA) (CANOCO v4.5, Lepš & Šmilauer 2003) was then used to determine the response of assemblages to environmental variables for each season. RDA was used after Direct Gradient Analysis (DCA), which was used to determine gradient lengths (Lepš & Šmilauer 2003). The species data were $\log_{10}$ transformed before analysis to moderate for the effects of rare and highly abundant morpho species (Clarke & Warwick 1994). The significance of the variables was tested with the Monte-Carlo permutation test (Lepš & Šmilauer 2003). For climatic data, a set of eight variables was used and their significance tested with Monte-Carlo permutation tests. Because of the collinearity of the variables, only five variables, amount of rainfall, relative humidity of the air, minimum temperature of the air, solar radiation and wind speed, all averaged over the sampling period, were used in the model and their significance was tested with a Monte-Carlo permutation tests.

Cluster analysis was performed to group sites according to the assemblage structure in PRIMER v5 (Clarke & Gorley 2001), using Bray-Curtis similarity matrices (Clarke & Warwick 2001). Abundance data were square-root transformed to a common down-weighting of rare and abundant species (Clarke & Warwick 2001). The Bray-Curtis similarity matrix was used in an ordination plot using non-metric multidimensional scaling (MDS) (Clarke & Gorley 2001; Clarke & Warwick 2001) to determine stress values. A stress function assesses how well the two-dimensional plot represents the actual sample relationship. A low stress value means the representation of samples on ordination is accurate (Clarke & Warwick 2001). Analysis of similarity (ANOSIM, 999 permutations) was used to test for significant differences between assemblages (Clarke &

Gorley 2001; Seymour & Dean 1999) using the Bray-Curtis similarities. Invertebrate assemblages from each land use were compared using the similarity percentage (SIMPER) programme in PRIMER v5 (Clarke & Gorley 2001) to determine species responsible for differences between sites (Seymour & Dean 1999). SIMPER calculates the percentage dissimilarity contributed by ground dwelling invertebrate species between land use types. The contribution of invertebrate species to the dissimilarity in assemblages is given as a cumulative value, starting with the highest dissimilarity percent contributed to the least dissimilarity contributed. Only the top five ground-dwelling invertebrate species contributors to the dissimilarity between land uses will be considered for each season (Seymour & Dean 1999).

3.3 Results

3.3.1 Seasonal differences

Total Species richness, abundance, diversity and evenness across seasons.

In autumn and spring, a total abundance of 2 759.22 ± 5 037.45 (Mean ± Standard deviation) and 656.56 ± 410.19 ground-dwelling invertebrates were captured respectively (Table 3.1). The highest numbers of individuals were captured in summer (3 667.67 ± 5 192.93) and autumn (2 759.22 ± 5 037.45) and the least in winter (306.33 ± 192.77). (Kruskal-Wallis H-Statistic) KW-H $_{(3, 36)}$ = 21.641, p = 0.0001) (Table 3.1). Species richness was highest in summer (26.44 ± 5.50) and was least in winter (14.33 ± 6.18), (KW-H $_{(3, 36)}$ = 9.721, p = 0.021). There were no significant differences in Shannon-diversity indices across seasons (KW-H $_{(3, 36)}$ = 2.147, p = 0.542) and species evenness (KW-H $_{(3, 36)}$ = 1.268, p = 0.737).

Relative abundances of ground-dwelling invertebrate orders excluding Hymenoptera: Formicidae across seasons

Abundance of Coleoptera (KW-H $_{(3, 12)}$ = 6.343, p = 0.096) was highest in summer. This was as a result of increased abundances of Tenebrionidae this season (Appendix A).

Though the differences were not significant (Figure 3.4A), Coleoptera abundances were higher in spring than in autumn and winter and this was because of increased abundances of Carabidae (Appendix A). Solifugae (KW-H $_{(3, 12)}$ = 5.071, p = 0.168) were least abundant in spring, Araneae (KW-H $_{(3, 36)}$ = 6.641, p = 0.084) were least abundant in summer while Collembola (KW-H $_{(3, 12)}$ = 3.932, p = 0.269) were more abundant in spring (Figures 3.4A and 3.4B). Scorpiones and Thysanura were only present in summer and Blattodea were absent in autumn and winter (KW-H $_{(3, 12)}$ = 5.228, p = 0.156) (Figures 3.4A and 3.4B). It should be noted that these significant results which could not be picked up by Kruskal-Wallis test were detected by Mann-Whitney U-test results, as depicted in figure 3.4A.

Relative abundances of Formicidae across seasons

Monomorium sp.4 (Hymenoptera: Formicidae) (Mon4, Appendix A) had significantly higher abundances in summer compared to the other seasons (KW-H $_{(3, 12)}$ = 27.461, p = 0.000), *Monomorium* sp.2 (Hymenoptera: Formicidae) (Mon2, Appendix A) was significantly abundant in autumn (KW-H $_{(3, 12)}$ = 18.922, p = 0.003). In winter, abundances of these species were low. *Camponotus* sp.3 (Hymenoptera: Formicidae) (Cam3, Appendix A) was the only species with the highest abundance in winter, though this was not significantly different from its abundance in spring (KW-H $_{(3, 12)}$ = 14.757, p = 0.002) (Table 3.2).

Species richness of ground-dwelling invertebrate orders across seasons

Hymenoptera (KW-H $_{(3, 12)}$ = 5.786, p = 0.016), Araneae (KW-H $_{(3, 12)}$ = 6.641, p = 0.843) and Coleoptera (KW-H $_{(3, 12)}$ = 6.998, p = 0.008) were the taxa with the highest richness across seasons. Hymenoptera species richness was lowest in winter while the number of species of Coleoptera was highest in spring (Figures 3.4C and 3.4D).

Table 3.1- Mean species richness S, Mean Shannon diversity index H, mean Shannon species evenness index E and mean total abundance N of all ground-dwelling invertebrates for the four seasons obtained using combined grid data. Means with different letters are statistically different (p< 0.05) across seasons.

Season	S ± SD	H ± SD	E ± SD	N ± SD
Summer	26.44 ± 5.50 **a**	1.25 ± 0.53	0.37 ± 0.15	3667.67 ± 5192.93 **a**
Autumn	22.00 ± 9.57 **ab**	1.05 ± 0.69	0.33 ± 0.18	2759.22 ± 5037.45 **a**
Winter	14.33 ± 6.18 **b**	0.92 ± 0.61	0.34 ± 0.19	306.33 ± 192.77 **b**
Spring	22.11 ± 8.55 **ab**	1.33 ± 0.71	0.44 ± 0.19	656.56 ± 410.19 **c**

A
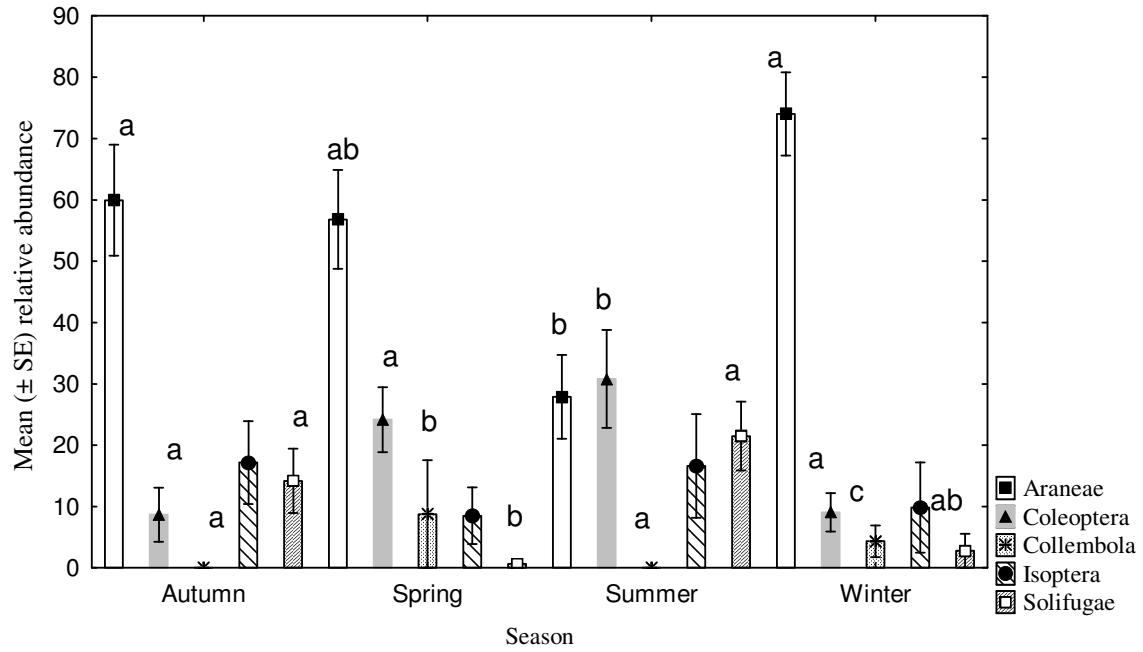
B
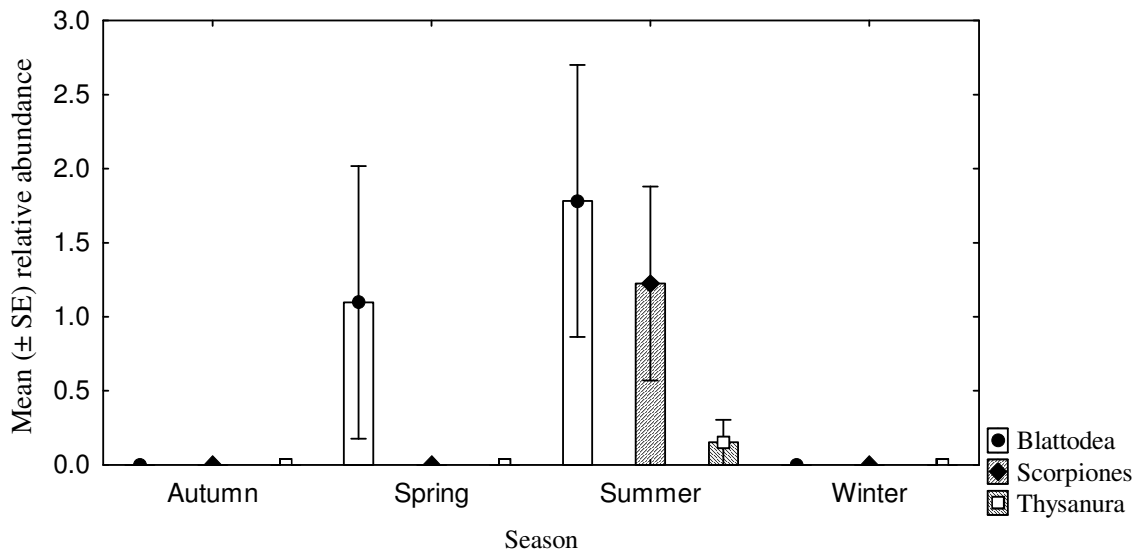
Figure 3.4: **A)** Mean relative abundance of the most common ground-dwelling invertebrate orders, **B)** the least common ground-dwelling invertebrate orders, for the four different seasons sampled, excluding ants (Hymenoptera: Formicidae), obtained using combined grid data. Orders showing significant variation as tested with Mann-Whitney U-test are shown with different lower case letters.

C
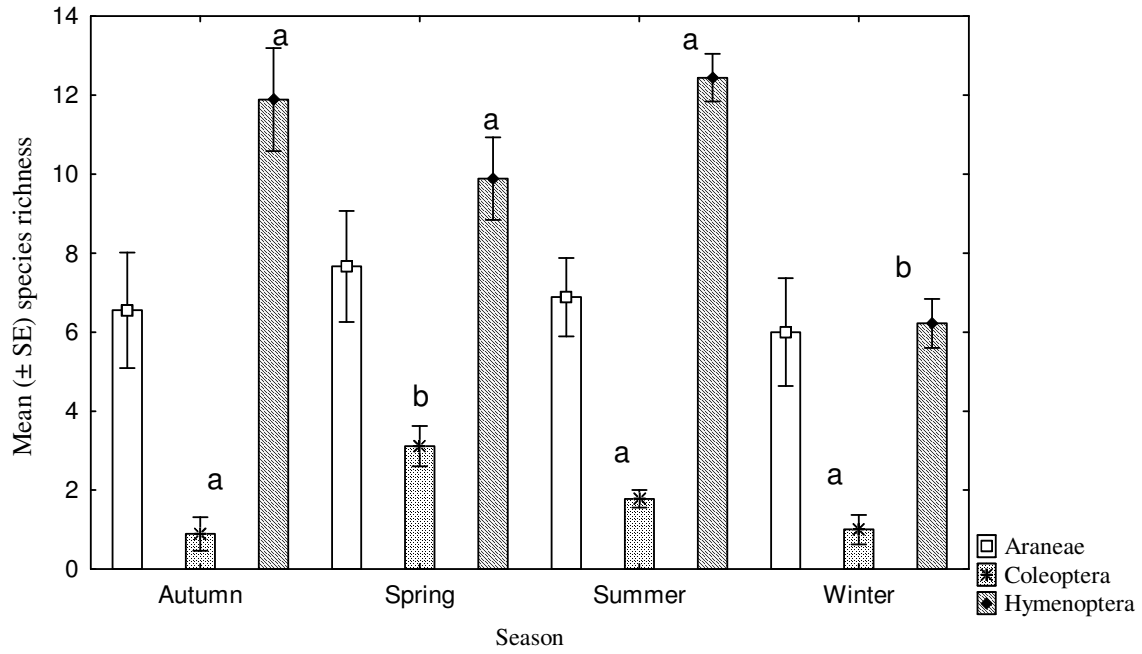
D
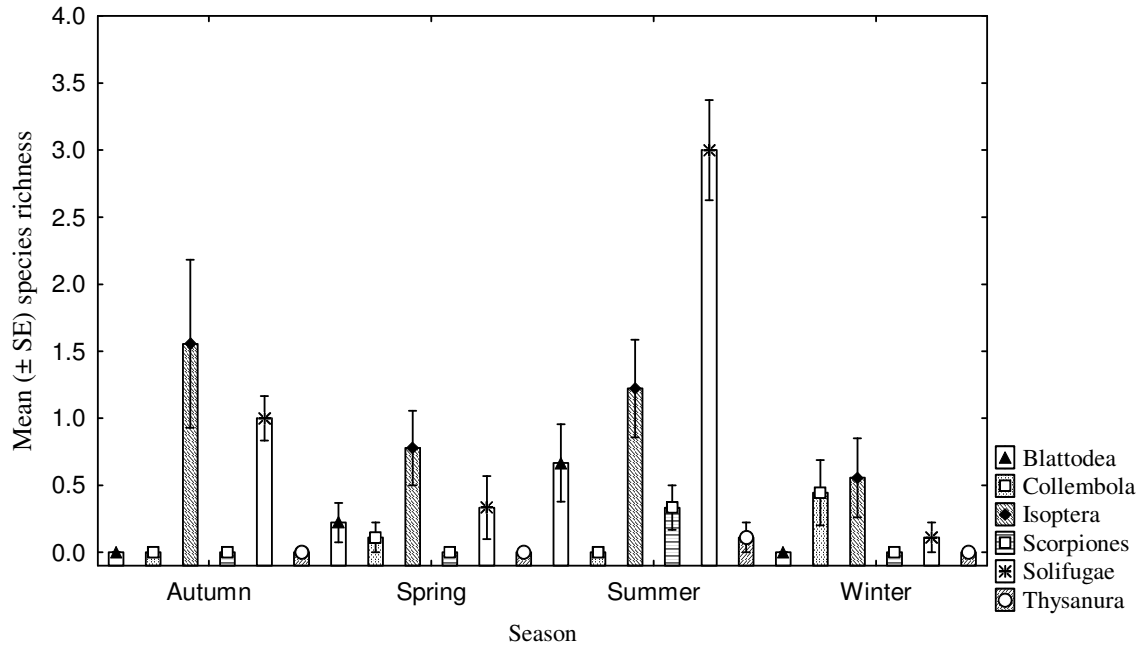
Figure 3.4: **C)** Mean species richness of the most common ground-dwelling invertebrate orders, **D)** the least common ground-dwelling invertebrate orders, for the four different seasons sampled obtained using combined grid data. Orders showing significant variation as tested with Mann-Whitney U-test are shown with different lower case letters.

Table 3.2: Means (±SE) relative abundance of the different ant (Hymenoptera: Formicidae) species caught in pitfall traps across seasons, obtained using combined grid data. Degree of freedom=3, n= 36. Sig. is the significance level; * p<0.05, ** p<0.01, *** p<0.001. Species showing significant differences across seasons as tested with Mann-Whitney U-test are shown with lower case letters. Ant species abbreviations given are explained fully in Appendix A. Species abbreviations are explained in full in Appendix A.

Sp.	Summer	Autumn	Winter	Spring	H -value	p- value	Sig.
Cam2	____	0.09 ± 0.05 **a**	0.02 ± .02 **ab**	____	9.641	0.0219	*
Cam3	____	____	0.73 ± 0.34 **b**	0.49 ± 0.31 **b**	14.757	0.0020	**
Cam6	0.40 ± 0.09 **ac**	0.36 ± 0.15 **a**	1.40 ± 0.44 **bc**	1.75 ± 0.47 **b**	11.839	0.0080	**
Cful	3.89 ± 1.68 **a**	1.60 ± 0.68 **a**	2.85 ± 1.80 **a**	13.99 ± 4.03 **b**	12.315	0.0064	**
Cre1	0.55 ± 0.27 **a**	2.93 ± 1.74 **a**	____	____	9.890	0.0195	*
Lep2	1.06 ± 0.48 **a**	0.50 ± 0.17 **a**	0.02 ± 0.02 **b**	0.19 ± .16 **ab**	11.149	0.0109	*
Mcap	0.47 ± 0.38 **a**	1.20 ± 0.59 **a**	____	____	19.962	0.0002	***
Mon2	0.001 ± 0.001 **b**	5.66 ± 2.20 **a**	0.10 ± 0.10 **b**	0.49 ± 0.42 **b**	18.922	0.0003	***
Mon4	25.77 ± 7.67 **c**	1.16 ± 0.58 **a**	____	____	27.461	0.0000	***
Obar	3.61 ± 0.85 **b**	1.80 ± 1.07 **a**	0.10 ± 0.10 **b**	1.04 ± 0.87 **a**	18.303	0.0004	***
Phe1	0.05 ± 0.68 **b**	____	____	____	9.524	0.0231	*
Tet1	1.26 ± 0.68 **c**	____	0.82 ± 0.49 **c**	10.35 ± 4.23 **b**	17.520	0.0006	***
Tqua	1.17 ± 0 54 **ab**	0.31 ± 0.08 **a**	0.09 ± 0.09 **c**	0.08 ± 0.4 **bc**	10.072	0.0180	*
Tsol	0.09 ± 0.03 **b**	0.71 ± 0.24 **a**	____	0.41 ± .21 **ab**	15.043	0.0018	**

Species assemblages

Across the seasons, the first RDA axis represents weather gradients of increasing and decreasing solar radiation, wind speed, minimum air temperature and relative humidity of the air and rainfall, and this was the only axis that accounted for variation in species-climatic relations (Figures 3.5A, 3.5B, 3.5C and 3.5D). In summer, autumn and winter, Weather conditions did not have a significant influence on invertebrate assemblages, (Monte-Carlo test F= 1.954, p = 0.05 for summer, F = 2.114, p = 0.058 for autumn, F = 1.853, p = 0.142 for winter). The contribution of weather variables to variation in species assemblages was nevertheless significant in spring (Monte Carlo F = 1.878, p = 0.0360).

In summer, *Crematogaster* sp.2 (Hymenoptera: Formicidae) (abbreviated as Cre2 in Appendix A), *Lepisiota* sp.2 (Hymenoptera: Formicidae) (Lep2), Hodotermitidae sp. 4 (Isoptera) (Hod4) and Araneae sp. 30 (Ara30) increased in abundances with hotter and windy conditions (Figure 3.5A). In winter, these conditions were associated with Araneae sp. 48 (Ara48) and *Camponotus fulvopilosus* (De Geer) (Hymenoptera: Formicidae) (Cful) while in spring the same conditions were associated with Carabidae sp. 1 (Coleoptera: Carabidae) (Car1), Araneae sp. 76 (Ara76), *Crematogaster* sp. 2, Araneae sp. 78 (Ara78), Araneae sp. 4 (Ara4) and *Monomorium* sp.3 (Hymenoptera: Formicidae) (Mon3) (Figure 3.5C and 3.5D). Abundances of *Anoplolepis steingroeveri* (Forel) (Hymenoptera: Formicidae) (Aste) and *Tetramorium* sp.1 (Hymenoptera: Formicidae) (Tet1) increased with increase in rainfall and relative humidity of the air in winter and spring (Figures 3.5C and 3.5D), and in autumn these species together with Araneae sp. 44 (Ara44) increased in abundance with hotter conditions (Figure 3.5B).

A

B

C

D
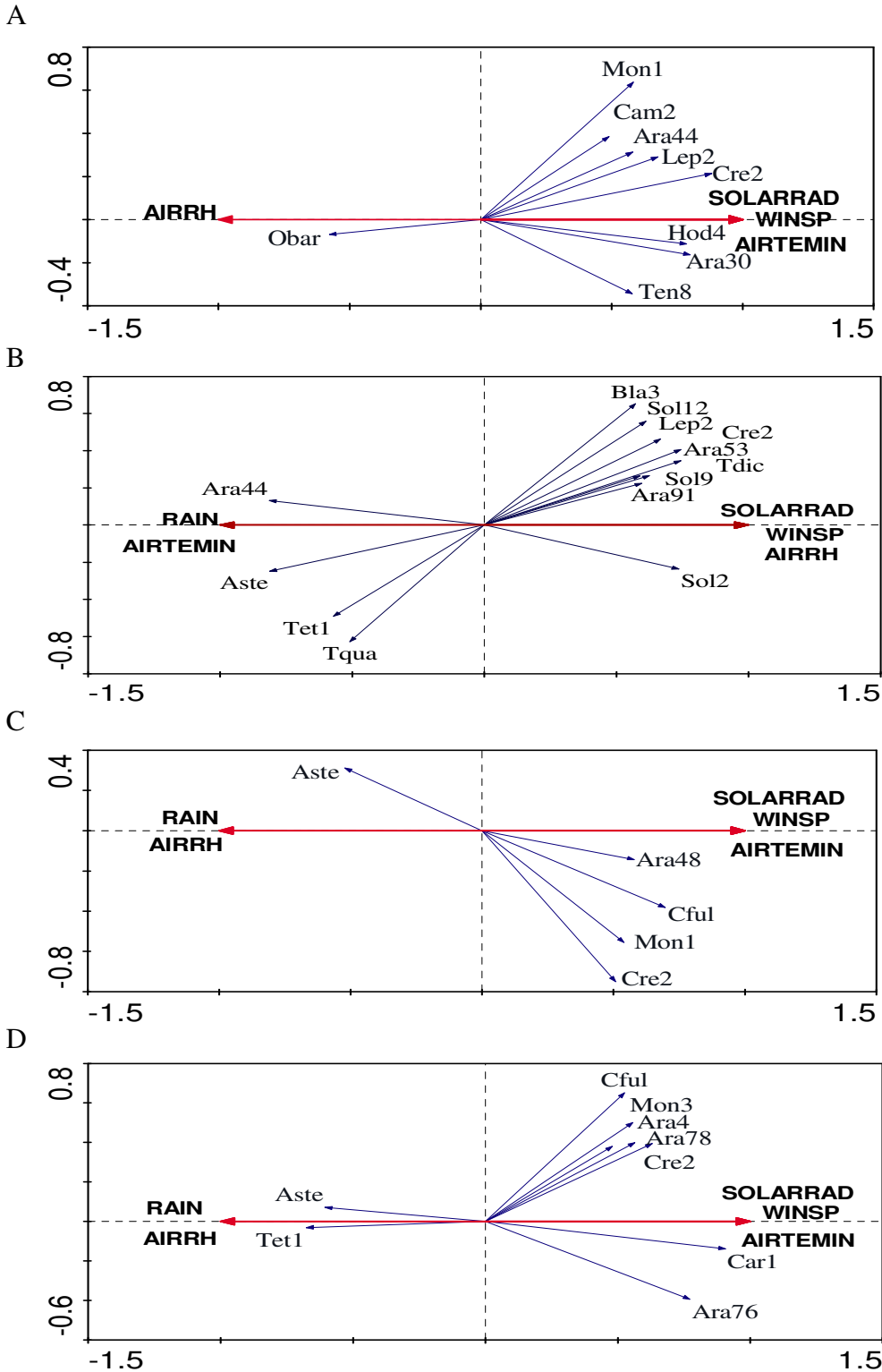
Figure 3.5: Redundancy analysis (RDA) biplot of species caught in pitfall traps and climatic variables for **A)** summer, **B)** autumn, **C)** winter and **D)** spring, all obtained using combined grid data. Only species that have their abundances explained by the first axis are shown (Appendix A). Climatic variable names: AIRTEMIN= Average minimum air temperature, WINSP= Average wind speed, SOLARRAD= Average solar radiation, RAIN= Rainfall and AIRRH= Relative humidity of the air.

3.3.2 Land use effects.

Vegetation and climatic changes

In summer, plant species richness was 2.7 ± 1.4 (mean ± standard deviation) in cultivated sites while plant species richness in the heavily and lightly grazed sites were 5.3 ± 1.7 and 7.2 ± 1.6 respectively (F $_{(2, 24)}$ = 19.000, p = 0.0001) (Table 3.3). In autumn there were 2.1 ± 1.2, 4.9 ± 1.5 and 5.8 ± 1.0 plant species in cultivated, heavily and lightly grazed sites respectively (F $_{(2, 24)}$ = 22.365, p = 0.0000). 8.1 ± 2.9, 9.2 ± 2.0 and 10.7 ± 1.9 plant species were recorded in cultivated, heavily and lightly grazed sites respectively in winter (F $_{(2, 24)}$ = 1.375, p = 0.272) while in spring, the plant species numbers were 4.8 ± 1.6, 9.2 ± 2.0 and 10.7 ± 1.9 for cultivated, heavily grazed and lightly grazed respectively (F $_{(2, 24)}$ = 24.481, p = 0.0000) (Table 3.3).

Table 3.4 shows mean percentage cover for annuals, rocks, grasses, bare ground, non succulent perennials and succulent perennials. In winter and spring, annuals had significantly higher cover in cultivated and heavily grazed sites than lightly grazed sites. (winter, Z = 2.975, p = 0.003, spring, Z = 3.417, p = 0.0006). Bare ground was highest in cultivated and lowest in lightly grazed sites through out all the seasons (summer, Z = 3.595, p = 0.003, autumn, Z = 2.932, p = 0.003, winter, Z = 3.146, p = 0.002 and spring Z = 3.591, p = 0.003). The opposite was true for rock cover (For summer, Z = 3.230, p = 0.001, autumn Z = 3.241, p = 0.001, winter Z = 2.419, p = 0.016 and spring, Z = 1.158, p = 0.247). Non-succulent perennials had significantly higher cover in cultivated compared to the grazed sites in summer (Z = 2.038, p = 0.042) and autumn (Z = 3.512, p = 0.0004). In winter the difference was only significant between cultivated and heavily grazed sites (Z = 2.083, p = 0.037) and in spring there were no significant differences (Z = 1.677, p = 0.093) (Table 3.4). The succulent perennials and succulent perennials with a height of less than 25 cm decreased significantly in the order lightly grazed, heavily grazed and cultivated for all seasons (Succulent perennials: summer, Z = 3.108, p = 0.004, autumn, Z = 3.700, p = 0.0002, winter, Z = 2.062, p = 0.039 and spring, Z = 2.708, p = 0.007, succulent perennials > 25 cm: summer, Z = 3.108, p = 0.002, autumn, Z = 2.762, p = 0.006, winter, Z = 2.809, p = 0.0005 and spring, Z = 3.547, p = 0.0004) (Tables 3.4 and

3.5). The opposite trend was observed for non-succulent perennials with a height of less than 25 cm, decreasing in the order: cultivated, heavily grazed and lightly grazed, though the difference between the cultivated and heavily grazed sites was only significant in autumn (Z = 3.382, p = 0.0007). Succulent perennials with a height greater than 25 cm were more dominant in lightly grazes sites, though only significantly different from heavily grazed in spring (Z = 3.138, p = 0.009) and autumn (Z = 3.112, p = 0.002).

Galenia africana L. had the high cover in cultivated sites for all seasons, as was the case for heavily grazed sites, except in spring when an annual sp.1 had the highest cover (Table 3.6). However, cover of *G. africana* was about two to three times more in cultivated than heavily grazed sites. *Eriocephalus africanus* L. (Asteraceae) had the highest cover in lightly grazed sites in autumn, winter and spring while in summer *Leipoldtia schultzei* Schltr. & Diels (Aizoaceae) was dominant.

Rainfall began peaking during the end of autumn (April to May) and reached a peak in winter (August) (Figure 3.6A). Air temperature and solar radiation were highest during summer sampling period, followed by autumn sampling period while these were minimal in winter (Figures 3.6B and 3.6C). The relative humidity of the air was lowest during autumn sampling (Figure 3.6D). Wind speed was constant during all sampling periods, (Figure 3.6E).

Table 3.3: Mean (±SD) and standard deviation of number of plant species recorded in the different land use types in the four seasons. These were obtained using combined grid data. Lower case letters indicate significant differences between land use types at p = 0.05, tested with one-way ANOVA.

Season	Cultivated	Heavily grazed	Lightly grazed
Summer	2.7 ± 1.4 **a**	5.3 ± 1.7 **b**	7.2 ± 1.6 **b**
Autumn	2.1 ± 1.2 **a**	4.9 ± 1.5 **b**	5.8 ± 1.0 **b**
Winter	8.1 ± 2.9	10.6 ± 3.6	9.4 ± 2.7
Spring	4.8 ± 1.6 **a**	9.2 ± 2.0 **b**	10.7 ± 1.9 **b**

Table 3.4: Mean (±SE) percentage cover of the different vegetation categories per land use across seasons, obtained using combined grid data. Lower case letters indicate significant difference between land use types per season at p = 0.05, tested with Mann-Whitney U-test. CL= cultivated, HG= heavily grazed and LH= lightly grazed. NSP= Non succulent perennial, SP= Succulent perennial. Su= summer, Au= autumn, Wi= winter and Sp= spring.

		Annual	Bare	Grass	NSP	Rock	SP
Su	**CL**	1.6 ± 0.73	54.2 ± 2.7 **a**	0.2 ± 0.2	43.6 ± 3.8 **a**	0.2 ± 0.2 **a**	0.2 ± 0.2 **a**
	HG	___	48.4 ± 3.5 **a**	0.7 ± 0.5	30.0 ± 4.5 **b**	7.8 ± 2.3 **b**	13.1 ± 4.4 **b**
	LG	___	28.2 ± 1.3 **b**	___	22.7 ± 2.2 **b**	9.6 ± 1.5 **b**	39.6 ± 2.2 **c**
Au	**CL**	___	62.9 ± 2.6 **a**	___	34.9 ± 2.9 **a**	1.6 ± 0.9 **a**	0.7 ± 0.5 **a**
	HG	___	52.9 ± 3.3 **b**	___	19.1 ± 2.1 **b**	12.7 ± 3.3 **b**	15.3 ± 2.1 **b**
	LG	___	33.3 ± 1.7 **c**	___	15.6 ± 2.4 **b**	12.9 ± 2.8 **b**	38.2 ± 3.6 **c**
Wi	**CL**	30.4 ± 5.6 **a**	34.0 ± 3.6 **a**	___	30.4 ± 4.6 **a**	2.2 ± 1.3 **a**	2.9 ± 1.4 **a**
	HG	27.1 ± 7.3 **a**	26.0 ± 4.8 **ab**	0.4 ± 0.3	18.4 ± 3.2 **b**	10.2 ± 2.3 **b**	17.8 ± 4.6 **b**
	LG	6.4 ± 3.2 **b**	15.6 ± 1.4 **b**	___	21.3 ± 3.2 **ab**	7.3 ± 1.8 **b**	49.3 ± 6.2 **c**
Sp	**CL**	21. 8 ± 5.2 **a**	36.9 ± 3.6 **a**	___	36.4 ± 3.3	2.9 ± 1.1	2.0 ± 1.6 **a**
	HG	20.0 ± 4.6 **a**	20.2 ± 3.2 **b**	5.1 ± 2.2 **b**	30.7 ± 4.8	5.8 ± 1.4	10.2 ± 3.4 **b**
	LG	4.4 ± 2.1 **b**	12.4 ± 2.0 **b**	0.9 ± 0.5 **ab**	26.2 ± 3.8	7.8 ± 2.5	48.2 ± 6.7 **c**

Table 3.5: Mean (±SD) percentage cover of non-succulent perennials (NSP) with height greater than 25cm, non-succulent perennials with height less than 25cm, succulent perennials (SP) with a height greater than 25cm and succulent perennials with a height less than 25cm per land use across seasons, obtained using combined grid data. Lower case letters indicate significant differences between land use types for each of the seasons at p = 0.05, tested with Mann-Whitney U-test. CL= cultivated, HG= heavily grazed and LH= lightly grazed

		NSP > 25cm	NSP < 25cm	SP > 25cm	SP < 25cm
Summer	CL	4.0 ± 5.1 **a**	39.6 ± 13.8 **a**	___	0.2 ± 0.7 **a**
	HG	2.4 ± 3.1 **a**	27.6 ± 14.1 **a**	3.6 ± 4.7 **b**	9.6 ± 12.4 **b**
	LG	16.2 ± 7.0 **b**	6.4 ± 5.5 **b**	9.6 ± 8.5 **b**	30.0 ± 8.2 **c**
Autumn	CL	2.9 ± 4.5 **a**	32.0 ± 10.7 **a**	0.2 ± 0.7 **a**	0.4 ± 1.3 **a**
	HG	3.1 ± 4.6 **a**	16.0 ± 4.8 **b**	4.0 ± 3.6 **b**	11.3 ± 5.7 **b**
	LG	10.2 ± 5.5 **b**	5.3 ± 3.5 **c**	10.27 ± 7.5 **c**	27.6 ± 10.5 **c**
Winter	CL	4.2 ± 4.1 **a**	26.2 ± 15.8 **a**	0.4 ± 0.9 **a**	2.4 ± 4.2 **a**
	HG	2.9 ± 5.8 **a**	15.6 ± 8.9 **a**	4.0 ± 5.8 **b**	13.8 ± 12.5 **b**
	LG	13.1 ± 7.9 **b**	8.2 ± 3.8 **b**	8.2 ± 6.4 **b**	41.1 ± 14.1 **c**
Spring	CL	4.2 ± 6.8 **a**	32.2 ± 13.7 **a**	0.7 ± 2.0 **a**	1.3 ± 2.8 **a**
	HG	3.6 ± 2.8 **a**	27.1 ± 14.7 **a**	1.6 ± 1.9 **a**	8.7 ± 9.9 **b**
	LG	16.4 ± 10.6 **b**	9.8 ± 7.2 **b**	12.2 ± 9.4 **b**	36.0 ± 15.2 **c**

Table 3.6: The two plant species with the highest cover per land use. These were also obtained using combined grid data. The percentage values are shown in brackets. CL= cultivated, HG= heavily grazed and LG= lightly grazed.

Land use	Season	Family	Species with highest percentage cover (in brackets)
CL	**Summer**	Aizoaceae	*Galenia africana* L. (35.8 %)
		Sterculiaceae	*Hermannia amoena* Dinter (4.7 %)
HG		Aizoaceae	*Galenia africana* L. (13.3 %)
		Molluginaceae	*Hypertelis salsoloides* Burch (5.1%)
LG		Aizoaceae	*Leipoldtia schultzei* Schltr. & Diels (19.8 %)
		Asteraceae	*Eriocephalus africanus* L. (14.7%)
CL	**Autumn**	Aizoaceae	*Galenia africana* L. (26.7 %)
		Asteraceae	*Chrysocoma ciliata*L. (4.9%)
HG		Aizoaceae	*Galenia africana* L. (10.9 %)
		Asteraceae	*Eriocephalus africanus* L. (5.8 %)
LG		Asteraceae	*Eriocephalus africanus* L. (12.2 %%)
		Aizoaceae	*Leipodeldtia schultzei* Schltr. & Diels (9.1 %)
CL	**Winter**	Aizoaceae	*Galenia africana* L. (24.7 %)
		Asteraceae	*Leysera tenella* D.C (8.0 %)
HG		Aizoaceae	*Galenia africana* L. (7.3%)
		Molluginaceae	*Hypertelis salsoloides* Burch (7.1%)
LG		Asteraceae	*Eriocephalus africanus* L. (12.7%)
		Aizoaceae	*Leipodeldtia schultzei* Schltr. & Diels (11.1 %)
CL	**Spring**	Aizoaceae	*Galenia africana* L. (30.9 %)
		Asteraceae	*Leysera tenella* D.C (12.7 %)
HG		Asteraceae	Non succulent perennial sp.1 (13.6 %)
		Scrophulariaceae	Annual sp.1 (9.1 %)
LG		Asteraceae	*Eriocephalus africanus* L. (11.6 %%)
		Aizoaceae	*Leipodeldtia schultzei* Schltr. & Diels (9.6 %)
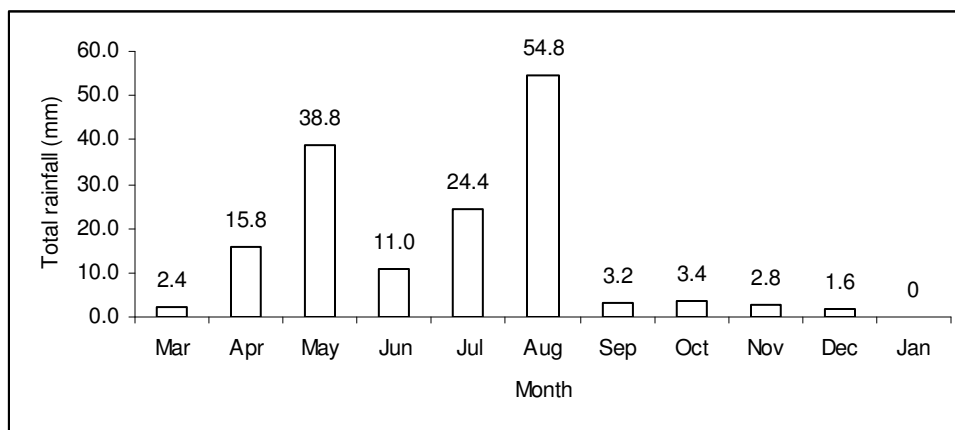
Figure 3.6A: Total rainfall in March to December 2006 and January 2007 in Paulshoek. Data from BIOTA weather station in Paulshoek, (30º 23' 41.1 ''S, 18º 17' 10.1''E).
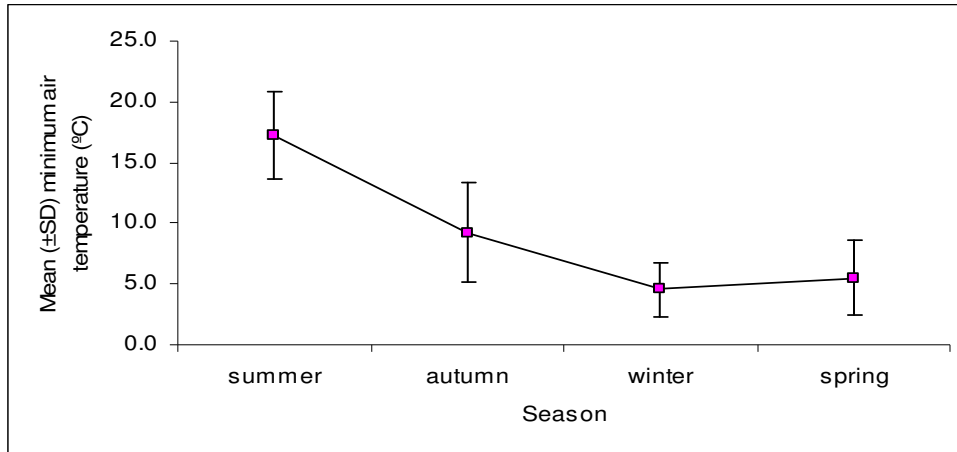
Figure 3.6B: Mean minimum air temperature (±SD) of seven-day sampling periods across seasonal samples. Data from BIOTA weather station in Paulshoek, (30º 23' 41.1 ''S, 18º 17' 10.1''E).
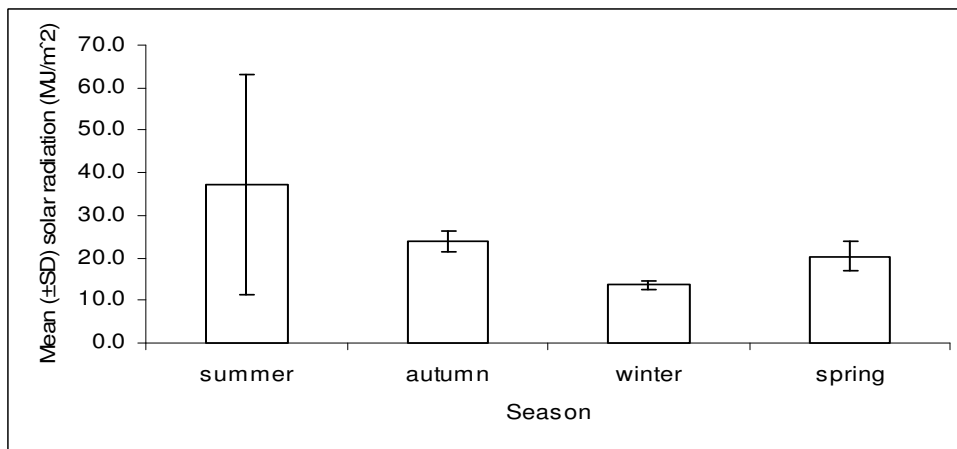
Figure 3.6C: Mean solar radiation (±SD) of seven-day sampling periods across seasonal samples. Data from BIOTA weather station in Paulshoek, (30º 23' 41.1 ''S, 18º 17' 10.1''E).
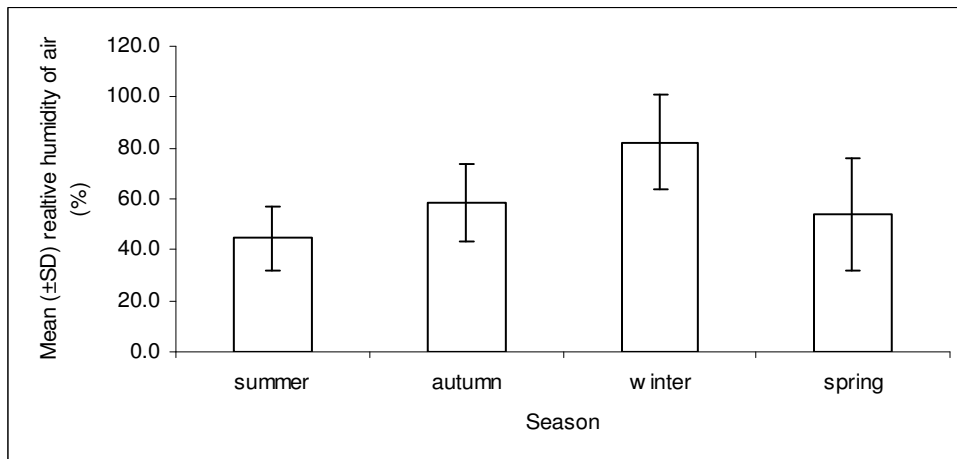
Figure 3.6D: Mean relative humidity of the air (±SD) of seven-day sampling periods across seasonal samples. Data from BIOTA weather station in Paulshoek, (30º 23' 41.1 ''S, 18º 17' 10.1''E).

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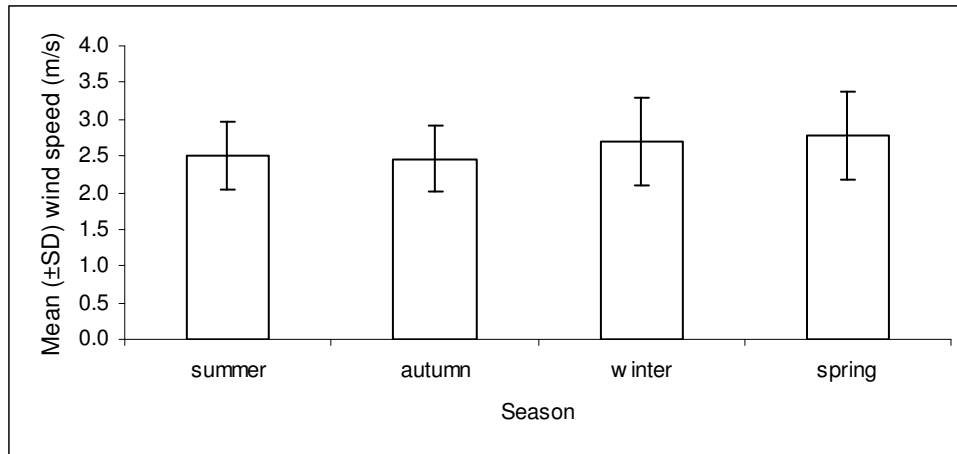
Figure 3.6E: Mean wind speed (±SD) of seven-day sampling periods across seasonal samples. Data from BIOTA weather station in Paulshoek, (30º 23' 41.1 ''S, 18º 17' 10.1''E).

Invertebrate species richness and abundance

Overall species richness differed significantly between land use types in autumn and winter. In autumn, richness was significantly lower in cultivated sites compared to the other sites ($F_{(2, 6)}$ = 14.246, p = 0.005) and in winter, the cultivated sites had significantly lower richness compared to lightly grazed sites ($F_{(2, 6)}$ = 7.929, p = 0.0207). Hymenoptera and Araneae were the taxa with highest richness across land uses (Figure 3.7). Generally species richness for Araneae was highest in lightly grazed sites (KW-H $_{(2, 9)}$ = 3.819, p = 0.148 for summer, KW-H $_{(2, 9)}$ = 7.322, p = 0.026 for autumn, KW-H $_{(2, 9)}$ = 5.956, p = 0.051 for winter and KW-H $_{(2, 9)}$ = 1.414, p = 0.493 for spring). Araneae (KW-H $_{(2, 9)}$ = 7.322, p = 0.026) and Tenebrionidae (KW-H $_{(2, 9)}$ = 7.322, p = 0.0257) were the only taxa for which richness differed significantly between land uses, however only in autumn (Figure 3.8). Richness of Araneae decreased in the order lightly grazed, heavily grazed and cultivated sites. Tenebrionidae had high richness in heavily grazed sites; though this was not significantly different from lightly grazed sites (Figure 3.8).

Ant abundances decreased from cultivated, heavily grazed and lightly grazed, and these were significantly more abundant in cultivated fields in summer (KW-H $_{(2,9)}$ = 7.200, p = 0.0273) while their richness was higher in lightly grazed and heavily grazed sites

compared to cultivated sites, though this was only significant in autumn (KW-H $_{(2,9)}$ = 4.355, p = 0.0369).

Araneae were more abundant in cultivated sites and significantly so compared to grazed sites in autumn (KW-H $_{(2, 9)}$ = 6.056, p = 0.048) (Figure 3.9, Appendix A). *Tetramorium solidum* (Emery) (Hymenoptera: Formicidae) (abbreviated Tsol in Appendix A) (KW-H $_{(2, 9)}$ = 6.161, p = 0.0459) and *Pheidole* sp.1 (Hymenoptera: Formicidae) (Phe1) (KW-H $_{(2, 9)}$ = 7.624, p = 0.022) showed significantly higher abundances in heavily grazed sites compared to the other land use types in summer (Figure 3.10). In autumn, *Camponotus* sp.4 (Hymenoptera: Formicidae) (Cam4) (KW-H $_{(2, 9)}$ = 7.624, p = 0.022) and *Crematogaster* sp.1 (Hymenoptera: Formicidae) (Cre1) (KW-H $_{(2, 9)}$ = 6.720, p = 0.035) were respectively most abundant in heavily grazed and lightly grazed sites (Figures 3.11A and 3.11B). Though not significant *A. steingroeveri* was predominant in cultivated sites, except in winter when its abundance was high in lightly grazed sites (KW-H $_{(2,9)}$ = 3.289, p = 0.193 for summer, KW-H $_{(2,9)}$ = 4.356, p = 0.113 for autumn, KW-H $_{(2,9)}$ = 2.489, p = 0.288 for winter and KW-H $_{(2,9)}$ = 0.267, p = 0.875 for spring) (Appendix A).
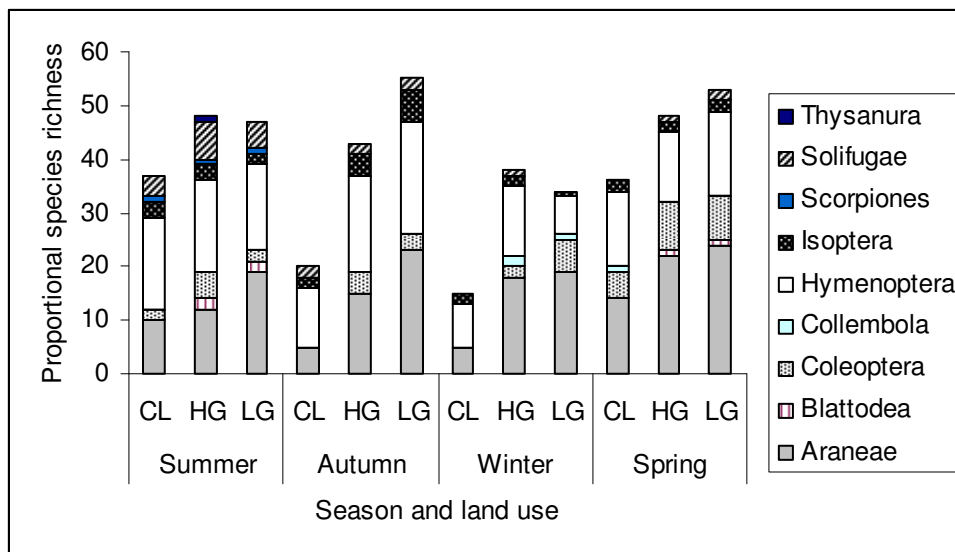
Figure 3.7: Summary of ground dwelling invertebrate species richness determined from pitfall trapping in each of the land uses across seasons. CL = Cultivated sites, HG = heavily grazed sites, LG = lightly grazed sites. Summary obtained using combined grid data..
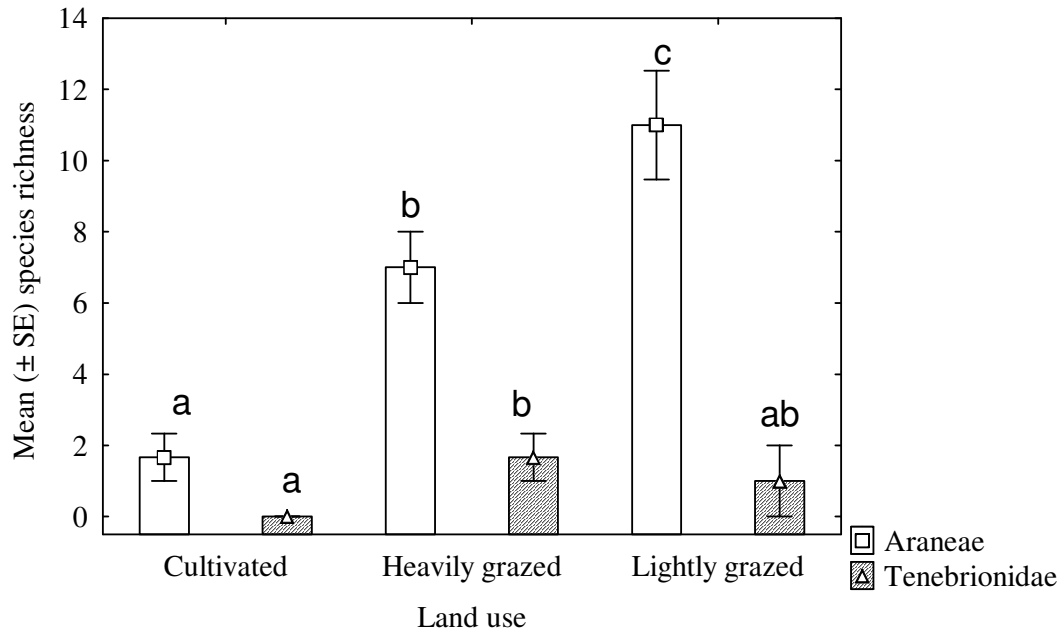
Figure 3.8: Results of Kruskal-Wallis and Mann-Whitney tests showing means and standard error of ground-dwelling taxa caught in pitfall traps showing significant differences between land uses in autumn. Significant differences are shown with lower

case letters. Results obtained using combined grid data.
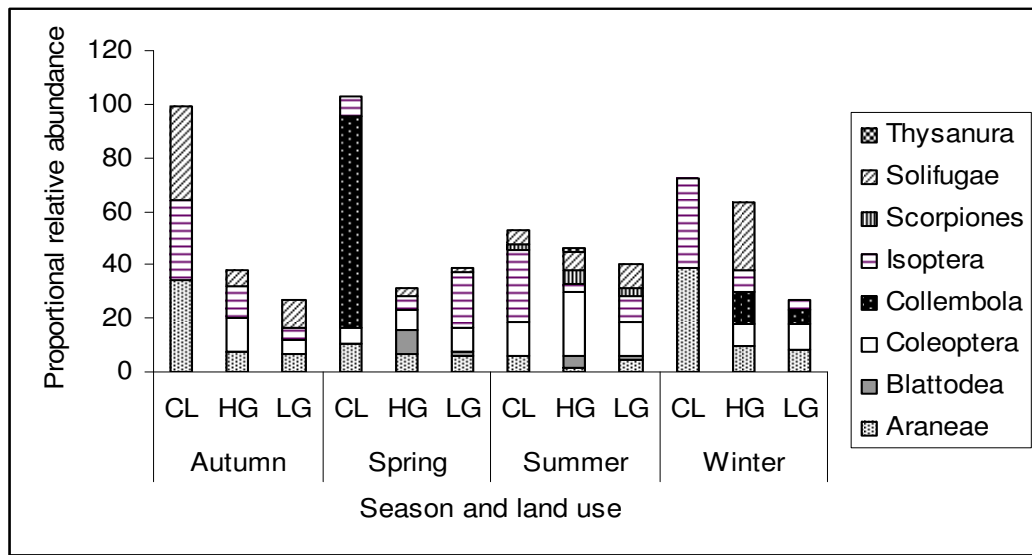
Figure 3.9: Summary of ground dwelling invertebrate relative abundances (excluding Hymenoptera: Formicidae) caught in pitfall traps in each of the land uses across the seasons. CL = Cultivated sites, HG = heavily grazed sites, LG = lightly grazed sites. Results obtained using combined grid data.
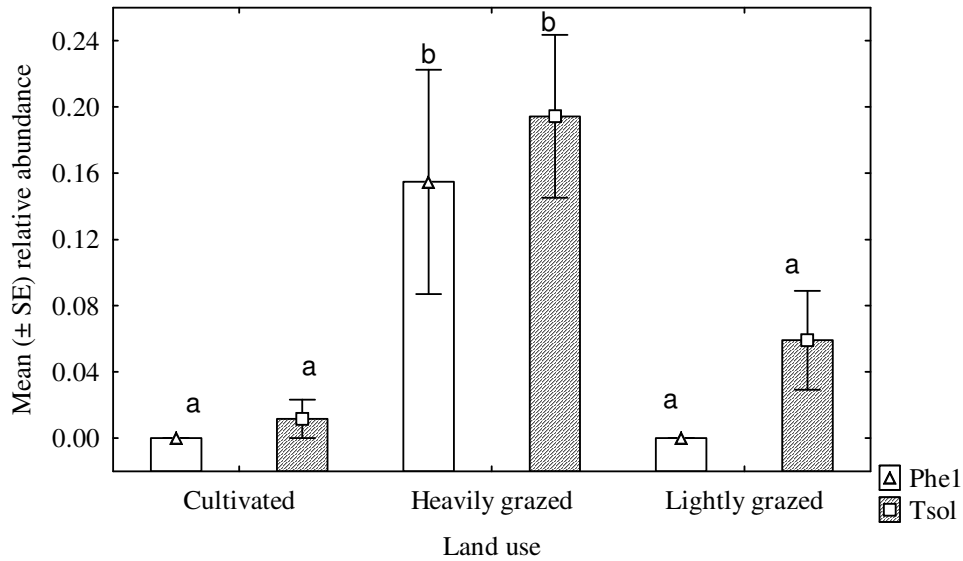
Figure 3.10: Results of Kruskal-Wallis and Mann-Whitney tests showing means and standard error of the relative abundance of ant species caught in pitfall traps in the three land uses in summer, obtained using combined grid data. Significant differences between land use abundances are shown with lower case letters. (Only significant results are shown).

A
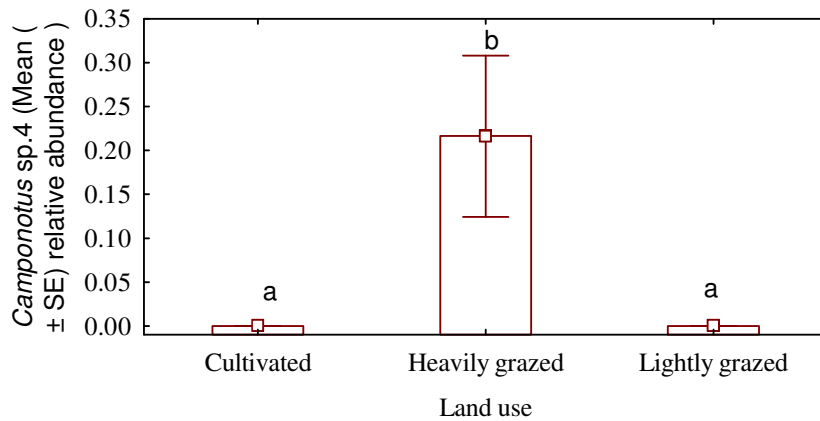
B
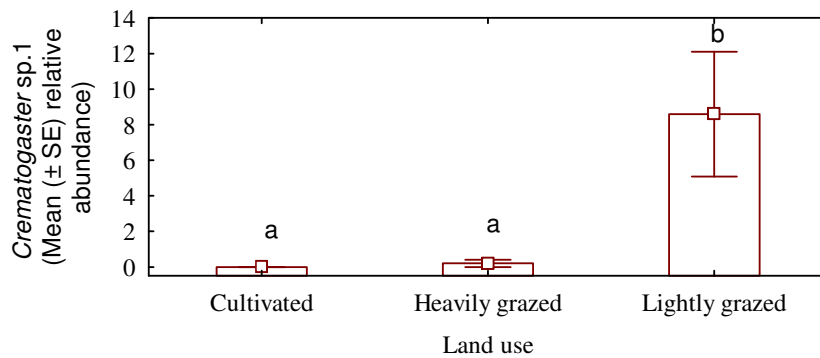
Figure 3.11:. Results of Kruskal-Wallis and Mann-Whitney tests showing means and standard error of the relative abundance of ant taxa caught in pitfall traps significant for land use for autumn. **A**) *Camponotus* sp.4, **B**) *Crematogaster* sp.1. Significant differences between land use abundances are shown with lower case letters. Results obtained using combined grid data.

Species assemblages and indicator species

Except for winter when species richness and abundances were lowest, assemblages differed significantly between land uses (R = 0.498, p = 0.021 and stress = 0.05 for summer, R = 0.35, p = 0.014 and stress = 0.06 for autumn, R = 0.276, p = 0.125 and stress = 0.06 for winter and R = 0.44, p = 0.021 and stress = 0.09 for spring). The assemblage structures between cultivated and lightly grazed sites were significantly different and highest for all seasons except winter, where the greatest difference was between cultivated and heavily grazed sites. In summer, R = 0.815, p = 0.01 between cultivated and lightly grazed, in autumn, R = 0.519, p = 0.01 between cultivated and lightly grazed sites, in winter, R = 0.593, p = 0.02 between cultivated and heavily grazed sites and in spring, R = 0.667, p = 0.01 between cultivated and lightly grazed.

In summer, the first RDA axis representing habitat gradients explained 34.9% of variation in the invertebrate assemblage (F = 1.073, p = 0.134) and variation explained by all axes was significant (F = 0.134, p = 0.009) (Figure 3.12A). The first and second axes together explained 52.1 % variance in species data. Axis two separates species associated with bare ground, perennials and annuals and those associated with succulents and rock cover. Two *Tetramorium* species (Tqua and Tsol), *A. steingroeveri* (Aste) and *Ocymyrmex barbiger* (Emery) (Hymenoptera: Formicidae) (Obar) were highly correlated with bare ground, perennial plant cover and annuals. Spiders were among taxa highly correlated with succulent plants and rock cover.

The first RDA axis for autumn explained 32.4% of the variation in the assemblage, (F = 1.920, p = 0.008) and together with the second axis explained 47.3% of the variation (Figure 3.12B). For all axes together, the variation explained in species-vegetation relation was significant (F = 2.012, p = 0.004). Axis 1 represents a gradient of increasing bare ground and perennial plant cover to the right and decreasing rock cover and succulents to the left. *A. steingroeveri* (Aste) and *O. barbiger* (Obar) increase with increasing bare ground and Araneae together with *Monomorium* species (Hymenoptera: Formicidae) increased with a decrease in succulents and rock cover.

In winter and spring, the habitat variables did not make a significant contribution in explaining assemblages (Figures 3.12C and 3.12D). For all axes together, F= 1.541, p = 0.0216 in spring and F = 0.930, p = 0.654 for winter. The first two axes in winter explained 22.6 % variation in assemblages and in spring, these explained 61.7%. *A. steingroeveri* (Aste) and *Tetramorium* sp. 1 (Tet1) dominated in the cultivated sites in winter and spring (Figures 3.12C and 3.12D). Certain species of Araneae (Ara34, Ara69 and Ara48), as well as *Monomorium* sp.1 (Mon1), *C. fulvopilosus* (Cful), *Camponotus* sp.6 (Cam6) and *Crematogaster* sp.2 (Cre2) increased with decreasing succulents and rock cover in winter (Figure 3.12C). In spring, the opposite was true. Most Araneae, *Monomorium* and *Camponotus* species were associated with increasing rock cover, succulents and grasses (Figure 3.12D).

Cluster analysis results yielded two main clusters for all seasons, with one outlying site, cultivated site 3 for summer and autumn and lightly grazed site 2 for winter and spring (Figures 3.13A, 3.13B, 3.13C and 3.13D). Clustering was dominated by both land use type and location of the sites. In summer, clusters were dominated by samples from similar locations while in autumn they were dominated by samples from the same land use types (Figures 3.13A and 3.13B). In spring and winter clusters were very similar, with cultivated sites 2 and 3 forming their own cluster and lightly grazed site 3 and heavily grazed site 3, both in Kleinfontein forming a similar cluster (Figures 3.13C and 3.13D).

Tables 3.7A, 3.7B, 3.7C and 3.7D show ground-dwelling invertebrate species responsible for dissimilarities between land uses in summer, autumn, winter and spring. Cultivated and lightly grazed sites had the greatest dissimilarity across all seasons while the least dissimilarity was between the grazed sites. *A. steingroeveri* contributed most of the dissimilarity between sites in summer, autumn and winter, together with *Monomorium* sp.4 in summer. In spring, *Tetramorium* sp.1 was the major contributor.

In summer, based on the indicator value method, *A. Steingroeveri*, *Tetramorium* sp.1, and *Tetramorium quadrispinosum* (Emery) (Hymenoptera: Formicidae) were characteristic indicators of cultivated. *Messor capensis* (Mayr) (Hymenoptera: Formicidae), *Pheidole* sp.1 and *T. solidum* were characteristic indicators for heavily grazed sites only one species of Araneae (Araneae sp. 94) was characteristic of lightly grazed sites (Table 3.8). *A. steingroeveri* which was dominant in cultivated sites in summer and autumn, (Appendix A) was an indicator for these sites. *M. capensis* which was an indicator for heavily grazed sites in summer was an indicator for lightly grazed sites in autumn (Table 3.8). In winter and spring, *Tetramorium* sp.1 was an indicator for cultivated sites and the two species of spiders were indicators for the grazed sites in these seasons.

A
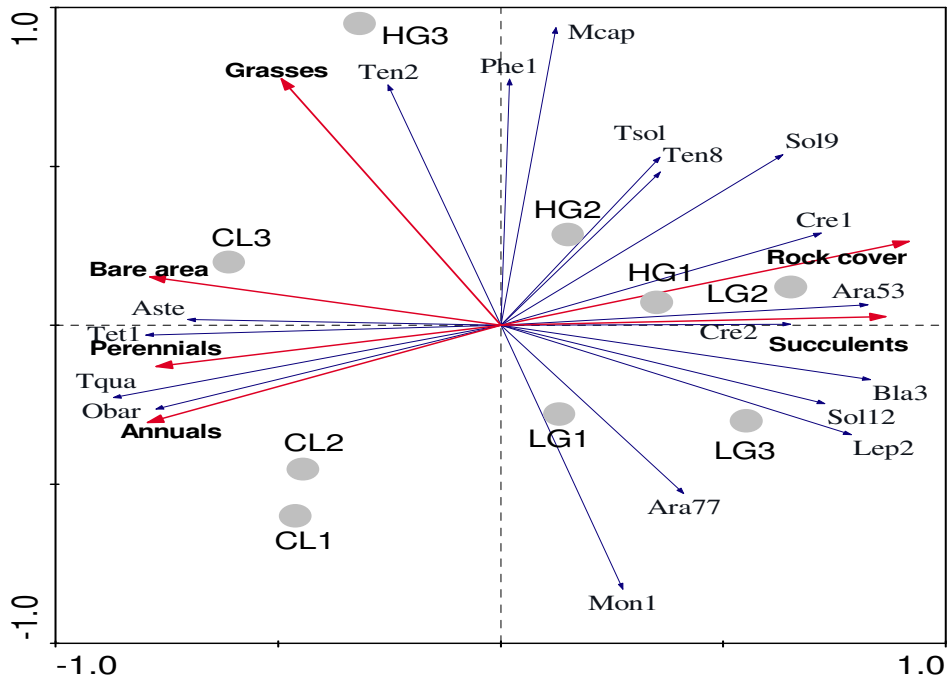
B
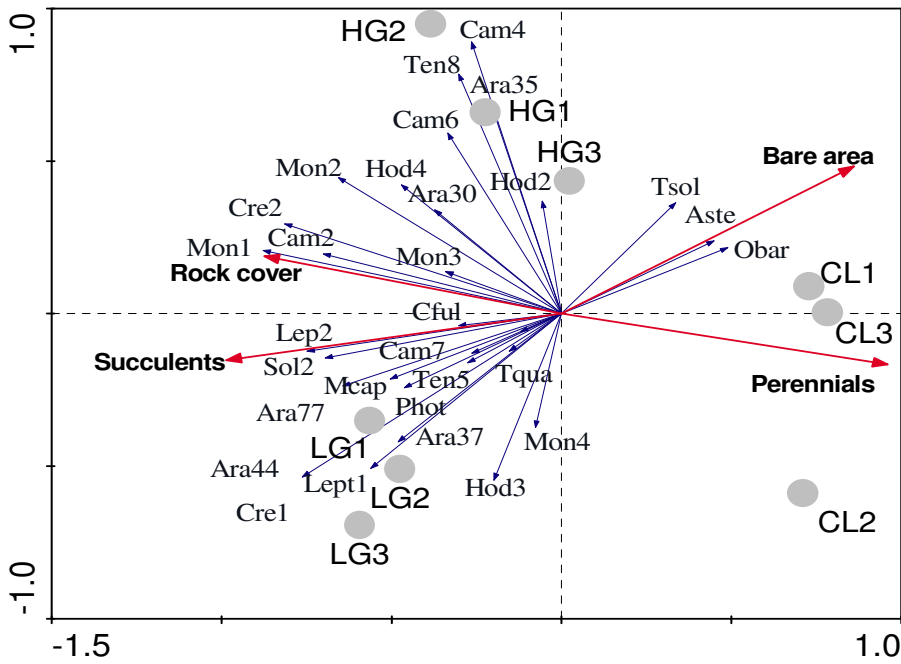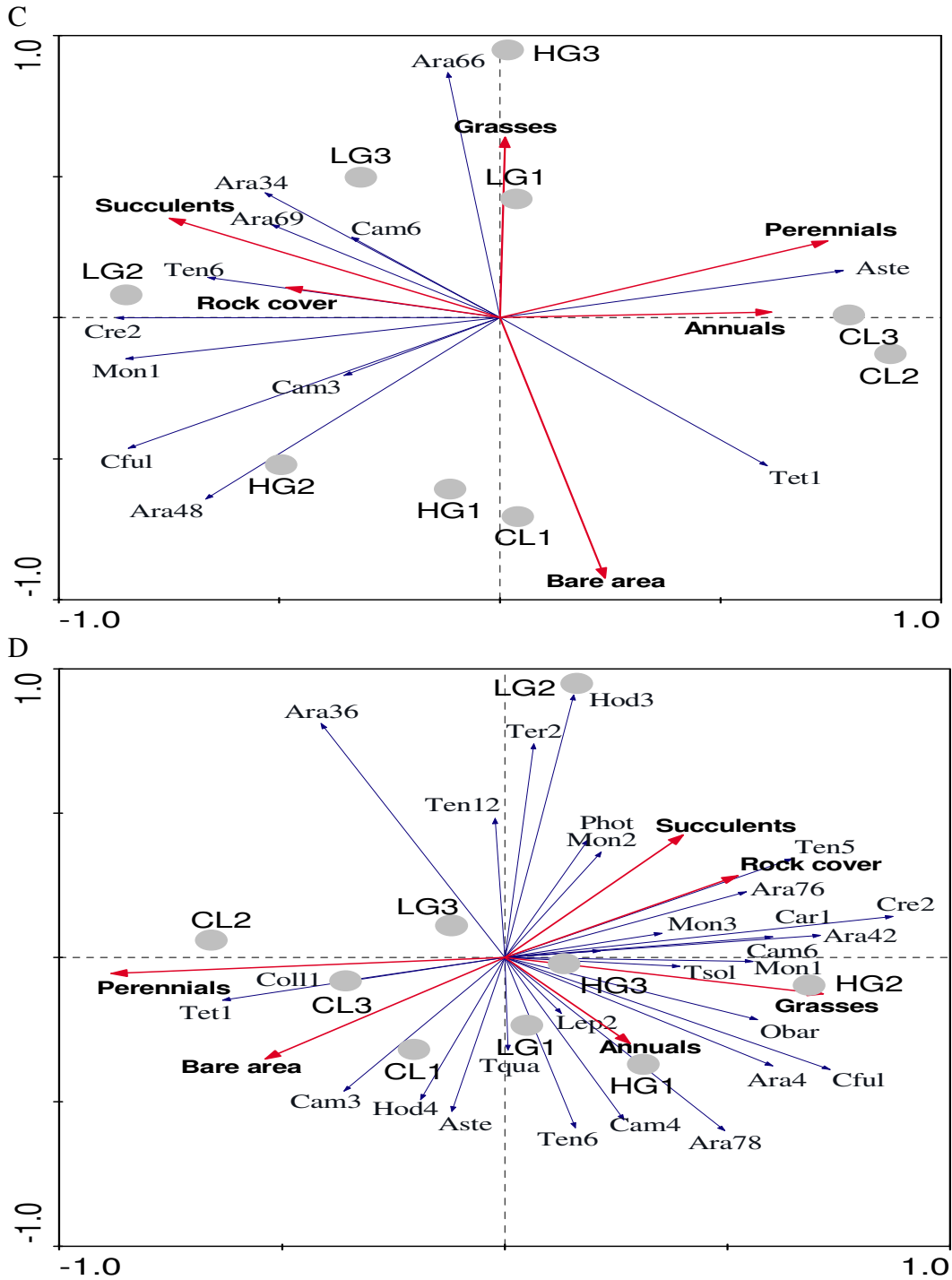
Figure 3.12. Redundancy analysis (RDA) triplot of ground dwelling species and habitat variables (Sites for illustrative purposes) for **A)** summer, **B)** autumn, **C)** winter and **D)** spring, obtained using combined grid data. For summer, only invertebrate species that account for 34% and more variation explained are shown. Site names: CL = cultivated, HG = heavily grazed, LG = lightly grazed. Numbers are the respective plot numbers for the different land uses. Succulents= succulent perennials and perennials= non succulent perennials.

A

LG2 Kuile
HG1 Kuile
LG1 Kuile
CL2 KLF
CL1 KLF
HG3 KLF
HG2 Kuile
LG3 KLF
CL3 KLF

20 40 60 80 100

Similarity

B

LG3 KLF
LG1 Kuile
LG2 Kuile
HG1Kuile
HG3 KLF
HG2 Kuile
CL2 KLF
CL1 KLF
CL3 KLF

20 40 60 80 100

Similarity

71

C

LG3 KLF
HG3 KLF
HG2 Kuile
HG1 Kuile
CL3 KLF
CL2 KLF
LG1 Kuile
CL1 KLF
LG2 Kuile

40   60   80   100

Similarity

D

HG2 Kuile
HG1 Kuile
CL1 KLF
LG3 KLF
HG3 KLF
LG1 Kuile
CL3 KLF
CL2 KLF
LG2 Kuile

40   60   80   100
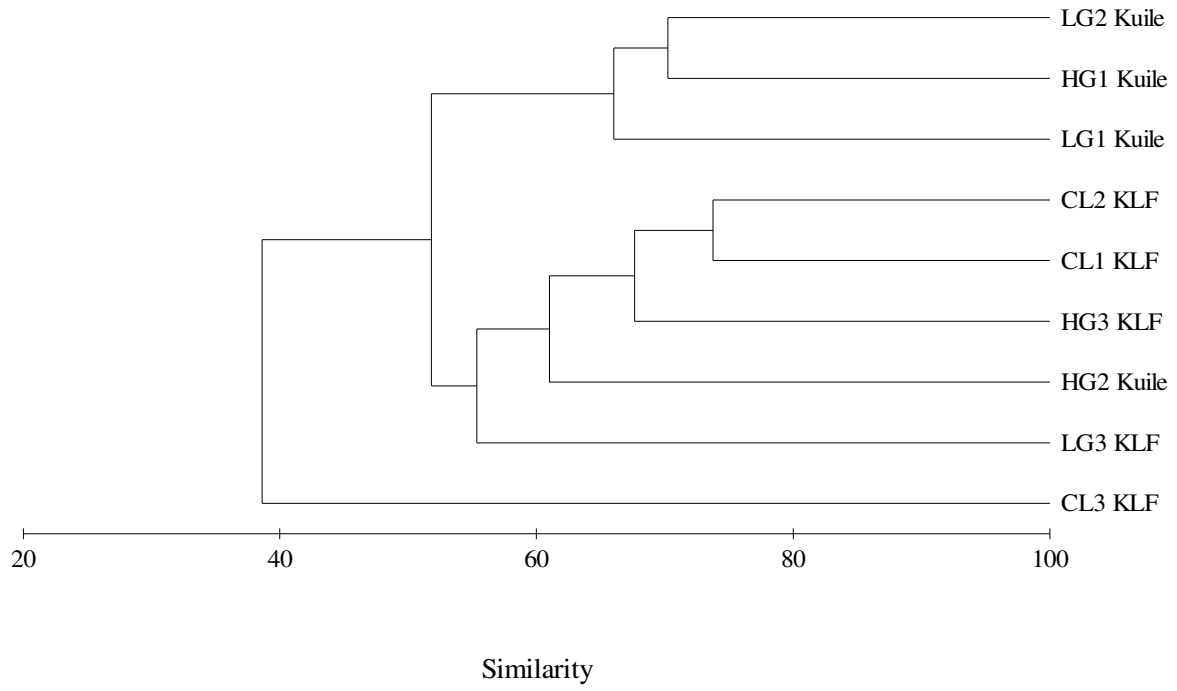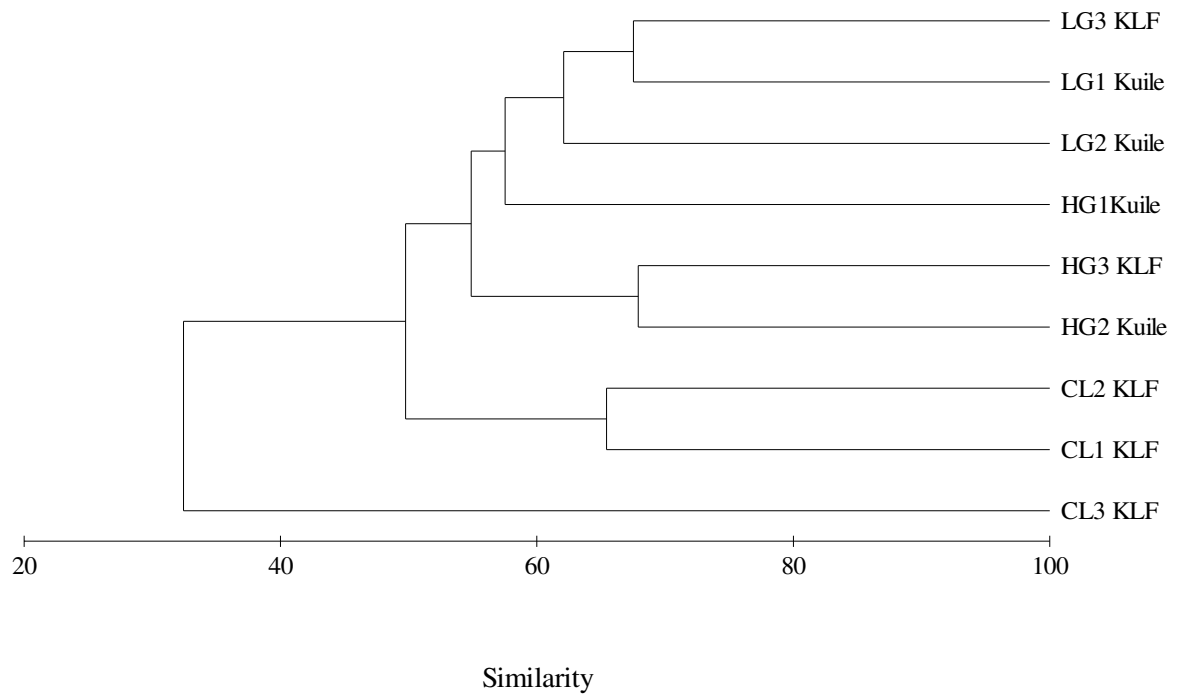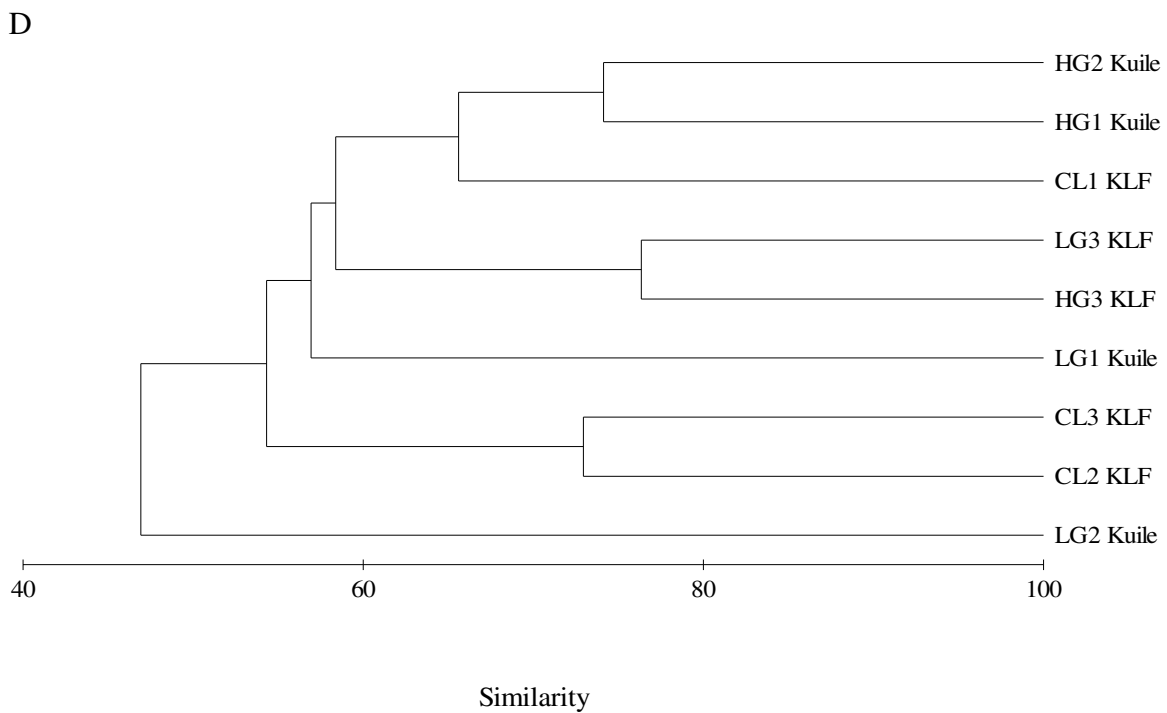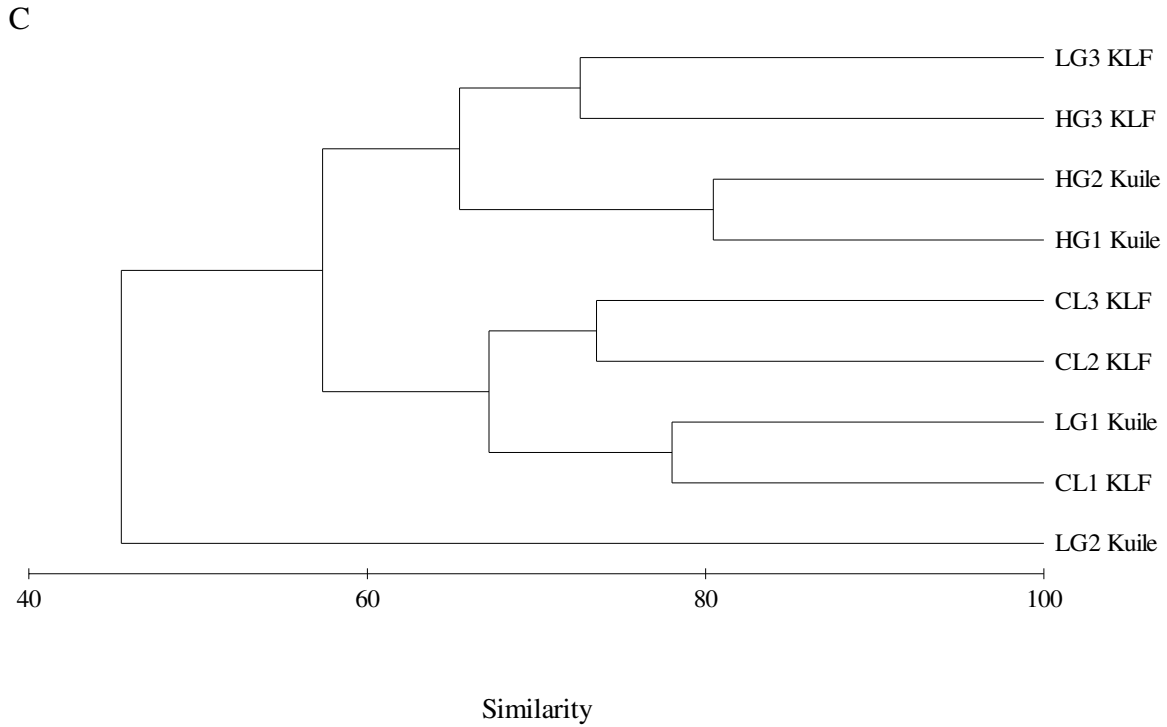
Similarity

Figure 3.13: Cluster analysis, as shown by Dendograms based on Bray-Curtis similarity matrix for the square root transformed ground dwelling invertebrate abundance data for **A)** summer, **B)** autumn **C)** winter and **D)** spring, obtained using combined grid data. Site names: CL = Cultivated, HG = heavily grazed, LG = lightly grazed. KLF=Kleinfontein and Kuile are the two locations where sampling was conducted.

Table 3.7A: Average dissimilarity between ground dwelling invertebrate assemblages trapped in pitfall traps from the different land uses. Taxa are arranged in order of decreasing contribution and only top five contributors shown (**summer**). Results obtained using combined grid data.

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
CL and HG	*Anoplolepis steingroeveri* (Forel)	38.95	38.95
Average	*Monomorium* sp.4	9.24	48.20
dissimilarity = 48.27	*Tetramorium* sp.1	7.96	56.16
	Crematogaster sp.2	6.79	62.94
	Tetramorium quadrispinosum (Emery)	5.66	68.60
CL and LG	*Anoplolepis steingroeveri* (Forel)	36.45	36.45
Average	*Crematogaster* sp.2	10.57	47.01
dissimilarity = 56.82	*Tetramorium* sp.1	8.73	55.74
	Monomorium sp.4	7.70	63.44
	Ocymyrmex barbiger (Emery)	5.73	69.17
HG and LG	*Monomorium* sp.4	19.07	19.07
Average	*Anoplolepis steingroeveri* (Forel)	15.13	34.20
dissimilarity = 44.29	*Crematogaster* sp.2	11.29	45.49
	Monomorium sp.1	4.61	50.10
	Lepisiota sp.2	3.52	53.62

Table 3.7B: Average dissimilarity between ground dwelling invertebrate assemblages trapped in pitfalls from the different land uses. Taxa are arranged in order of decreasing contribution and only top five contributors shown (**autumn**). Results obtained using combined grid data.

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
CL and HG	*Anoplolepis steingroeveri* (Forel)	38.54	38.54
Average	*Monomorium* sp.1	12.00	50.54
dissimilarity = 55.51	*Monomorium* sp.2	9.71	60.25
	Crematogaster sp.2	6.84	67.09
	Ocymyrmex barbiger (Emery)	3.46	70.55
CL and LG	*Anoplolepis steingroeveri* (Forel)	31.69	31.69
Average	*Monomorium* sp.1	10.55	42.24
dissimilarity = 56.68	*Crematogaster* sp.1	8.97	51.21
	Monomorium sp.2	5.68	56.89
	Crematogaster sp.2	4.34	61.23
HG and LG	*Anoplolepis steingroeveri (Forel)*	22.85	22.85
Average	*Crematogaster* sp.1	9.14	31.98
dissimilarity = 43.22	*Monomorium* sp.2	8.72	40.70
	Monomorium sp.1	6.90	47.60
	Crematogaster sp.2	6.37	53.97

Table 3.7C: Average dissimilarity between ground dwelling invertebrate assemblages caught from pitfall traps from the different land uses. Taxa are arranged in order of decreasing contribution and only top five contributors shown (**winter**). Results obtained using combined grid data.

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
CL and HG	*Anoplolepis steingroeveri* (Forel)	36.39	36.39
Average	*Crematogaster* sp.2	17.53	53.92
dissimilarity = 43.41	*Monomorium* sp.1	10.56	64.48
	Tetramorium sp.1	9.52	74.00
	Camponotus fulvopilosus (De Geer)	6.99	80.99
CL and LG	*Anoplolepis steingroeveri* (Forel)	34.59	34.59
Average	*Crematogaster* sp.2	20.15	54.75
dissimilarity = 47.40	*Tetramorium* sp.1	9.61	64.36
	Monomorium sp.1	5.75	70.10
	Araneae sp.34	5.16	75.27
HG and LG	*Anoplolepis steingroeveri* (Forel)	35.50	35.50
Average	*Crematogaster* sp.2	14.12	49.62
dissimilarity = 38.32	Araneae sp.34	6.60	56.22
	Monomorium sp.1	6.36	62.58
	Camponotus fulvopilosus (De Geer)	6.02	68.59

Table 3.7D: Average dissimilarity between ground dwelling invertebrate assemblages caught from pitfall traps from the different land uses. Taxa are arranged in order of decreasing contribution and only top five contributors shown (**spring**).Results obtained using combined grid data.

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
CL and HG	*Tetramorium* sp.1	16.47	16.47
Average	*Camponotus fulvopilosus* (De Geer)	14.49	30.96
dissimilarity = 43.13	*Crematogaster* sp.2	11.29	42.24
	Anoplolepis steingroeveri (Forel)	9.08	51.33
	Monomorium sp.1	6.22	57.55
CL and LG	*Anoplolepis steingroeveri* (Forel)	23.30	23.30
Average	*Tetramorium* sp.1	18.93	42.24
dissimilarity = 51.82	*Crematogaster* sp.2	6.95	49.19
	Camponotus fulvopilosus (De Geer)	5.65	54.83
	Monomorium sp.1	4.40	59.23
HG and LG	*Anoplolepis steingroeveri* (Forel)	28.08	28.08
Average	*Camponotus fulvopilosus* (De Geer)	13.55	41.63
dissimilarity = 43.22	*Monomorium* sp.1	5.62	47.25
	Monomorium sp.3	4.84	52.09
	Crematogaster sp.2	4.37	56.45

Table 3.8: Percentage indicator values (INDVAL > 70%) of ground-dwelling invertebrate species caught in pitfall traps for the different land use types across seasons. Results obtained using combined grid data.

Taxon	Species	% INDVAL		
		CL	HG	LG
Summer				
Formicidae	*Anoplolepis steingroeveri* (Forel)	88.1		
Formicidae	*Tetramorium* sp.1	95.9		
Formicidae	*Tetramorium quadrispinosum* (Emery)	84.2		
Formicidae	*Messor capensis* (Mayr)		89.7	
Formicidae	*Pheidole* sp.1		100.0	
Formicidae	*Tetramorium solidum* (Emery)		78.6	
Araneae	Araneae sp.94			81.8
Autumn				
Formicidae	*Anoplolepis steingroeveri* (Forel)	76.9		
Formicidae	*Camponotus* sp.4		100.0	
Formicidae	*Monomorium* sp.2		76.0	
Formicidae	*Crematogaster* sp.1			98.4
Formicidae	*Messor capensis* (Mayr)			72.3
Winter				
Formicidae	*Tetramorium* sp.1	91.3		
Araneae	Araneae sp.34			100.0
Spring				
Formicidae	*Tetramorium sp.1*	88.6		
Araneae	Araneae sp.42		72.7	

3.4 Discussion

3.4.1 Seasonal differences

The use of pitfall traps in sampling ground-dwelling invertebrates has been criticized (Majer 1997) for several reasons. These traps have been found to under-sample most of the ant communities (Sunderland *et al*. 1995; Majer 1997), reflecting in most cases activity pattern of ground-dwelling taxa (Luff 1975; Majer 1997) and leading to biased results that are determined by ground cover (Luff 1975). However, this method still remains the most widely used and serves to trap a large number and wide variety of ground-dwelling invertebrate species (Lindsey & Skinner 2001; Harris *et al*. 2003) and are useful for comparative purposes.

There is limited knowledge about what is happening to invertebrate communities worldwide as a result of anthropogenic activities, the major reason being lack of taxonomic expertise and time and financial constraints (Oliver & Beattie 1996a; Derraik *et al*. 2002). To allow conservation efforts to go ahead, alternatives are required. One of the options is to use the Recognisable Taxonomic Units (RTUs) (Oliver & Beattie 1993; New 2000). Despite the strong and rigorous debate surrounding the use of Morphospecies (Oliver & Beattie 1993; Oliver & Beattie 1996a, b; Oliver & Beattie 1997; Goldstein 1997; Goldstein 1999), this method has been found useful and accurate providing the aims of the study are not compromised (Derraik *et al*. 2002). However, the use of RTUs is misleading in cases where species are cryptic, that is, if it is difficult to readily separate species based on their morphological characters (New 2000). Ensuring consistency when using RTUs is one major problem that usually leads to clumping (more than one species classified as a single morphospecies) and hence reduced underestimation of species richness (Derraik *et al*. 2002) or splitting (one species classified as more than one species), as a result, for instance, of sexual dimorphism and overestimation of species richness (Oliver & Beattie 1993; Derraik *et al*. 2002). This was of particular importance in this study where species had to be compared with the voucher morphospecies from the previous seasons. Although the use of RTUs provides a rapid bioassessment for invertebrates, Oliver & Beattie (1996a) maintain that this technique requires the use of nonambiguous features which can easily and quickly be utilized. In this study, ambiguity could have compounded with more species being collected during the different seasons, leading to the common clumping and splitting problems. The chance of not recognizing a previously recorded RTU increases with increasing number of specimens (Oliver & Beattie 1996a). Despite all these, the use of RTUs is becoming a popular and useful technique (Fabricius *et al*. 2003).

The highest number of individuals was captured in summer and these were significantly different from the least obtained in winter and to those obtained in spring. Species richness was highest in summer and significantly differed to richness in winter. Formicidae were the most abundant taxon across all seasons with a peak in summer and a distinct trough in winter and Araneae was lowest in summer, when Coleoptera were the

second most abundant. The abundance of Araneae peaked in winter while richness was the same across seasons. Collembola were only present in winter and spring. Coleoptera abundances were significantly predominant in summer compared to the other seasons and richness peaked in spring. Among other taxa with high abundances in summer were Solifugae. Blattodea, Scorpiones and Thysanura were only present in very low abundances.

Seasonality in ground-dwelling invertebrates is common and this is a complex phenomenon that can be explained by both biotic and abiotic factors (Retana & Cerdá 2000; Pinheiro *et al*. 2002; Lindsley & Skinner 2001; Netshilaphala *et al*. 2005). The substantial difference in species richness and abundance of ground-dwelling invertebrates across seasons as shown by Figures 3.4A, 3.4C and 3.2, are not uncommon in arid areas (Sassi *et al*. 2006; Netshilaphala *et al*. 2005) and many Mediterranean regions (Boonzaaier 2006; Andersen 1986). Ant abundances peaked in summer and with a distinct trough in winter, a pattern which has been found in many other studies (Andersen 1986; Lindsey & Skinner 2001; Botes *et al*. 2006). In particular, during the hot and windy summer conditions, *Crematogaster* sp.2 and *Lepisiota* sp.2 together with Hodotermitidae sp. 4 and Araneae sp. 30 increased in abundances. Species such as *A. steingroeveri* showed different responses to weather changes, increasing in the colder winter and spring seasons in response to rainfall and relative humidity, while in the hotter autumn season, its abundance increased in response to hotter temperatures. These results are in agreement with Rissing (1988) and Andersen (1986). The latter author attributed these seasonal cycles according the prevailing weather conditions to be caused by reductions in insolation during the colder seasons which depresses activity (Kerley 1991), while Rissing (1988) attributes increased abundances in hot seasons to increased activity to maximise collection of the scarce food resources.

The ant assemblages were dominated by members of Myrmicinae and Formicinae. These two subfamilies are known to dominate ant communities in the Karoo and other arid areas (Lindsey & Skinner 2001; Marsh 1988). The myrmecochorous species *A. steingroeveri*, *M. capensis* and *T. quadrispinosum* (Botes *et al*. 2006; Hölldobler &

Wilson 1990) showed a marked increase in abundance in summer. Andersen (1997) regards these species as thermophilic as they favour hot habitats. Kerley (1991) also found seed removal by ants, mainly *Messor* species to be significantly higher in Hopedale, Succulent Karoo, in summer and autumn than in winter and attributes the low seed removal by ants in winter to cold, which depressed their activity. Similarly, Rissing (1988) showed that foraging activity of *Pogonomyrmex rugosus* (Formicidae) was high during dry periods when seed shortage was high. *M. capensis*, a major seed collector in the Karoo collects seeds only during warmer months of the year (Milton & Dean 1993). Flowering of plants at the study area occurred after winter rains and in spring. Seed availability therefore increased in spring and summer, increasing abundances of myrmecochorous taxa. Increased abundances in summer were therefore a result of hot temperatures and seed availability.

The influence on members of Solifugae was only in autumn where their abundances increased with solar radiation, wind speed and relative humidity of the air. This arid and semi-arid adapted predator group (Dean & Griffin 1993) is known to favour hot conditions and that could explain their high abundances during the hot seasons. Dean & Griffin (1993) also found increased soil-surface temperature to favour activity of certain species of Solifugae. The authors maintain that the possibility exists that species of Solifugae that tolerate high soil-surface temperature are those that prey on species which have been severely handicapped by thermal stress, hence prey specialisation may sort the activity pattern of Solifugae species.

Soil moisture and humidity are important in determining abundances and distribution of most taxa such as Collembola (Verhoef & van Selm 1983). Increased abundances of Collembola in spring and winter can partly be attributed to the increased moisture content in these seasons. Collembola are also known to form an important prey for most species of Araneae (Lawrence & Wise 2004; Moulder & Reichle 1972), hence peaks in Araneae abundances in winter could have been a result of the associated increase in Collembola numbers in this season. Kampichler & Geissen (2004) found that the population

dynamics of prey and predators for soil surface species influence each other, with predators increasing with increases in prey numbers.

Abundance of Tenebrionidae increased in summer, as was found by (De Los Santos *et al*. 2006) in one species of Tenebrionidae; *Pimelia canariensis*. Tenebrionidae are predominant in arid and semi-arid regions and are able to withstand extremely high temperatures (Cloudsley-Thompson 2001). Their lifecycles are linked to the hot temperatures (De Los Santos *et al*. 2006) and emergence of adult and population sizes are highly influenced by temperature (De Los Santos e*t al*. 1988). Tenebrionidae sp. 8 which contributed to significantly high abundances in summer compared to the other seasons was the only species of Tenebrionids in the RDA results influenced by solar radiation, air temperature and wind speed.

Carabidae abundances peaked in spring in this study. These are known to overwinter and emerge during the following spring (Holland & Reynolds 2003) and their abundances are merited to the presence of organic matter (Ferguson & McPherson 1985). This seasonality in Carabidae has also been shown for overwintering larval stage (Noordhuis *et al*. 2001). In the Cape Floristic Region, Boonzaaier (2006) found the litter layer to increase during winter. In this study, though organic matter content was not determined, the increased cover of annual plants in winter and spring is likely to have increased the organic matter content and the associated increase in Carabidae richness and abundances. Carabidae are predators with a wide range of prey including Collembola and Hemiptera: Aphididae (Lӧvei & Sunderland 1996). Their increased abundance could be a result of increased numbers of Collembola. Their reproductive success is also known to depend on food supply, with increase in reproduction with increasing food availability for egg-laying (Lӧvei & Sunderland 1996).

Some of the ground-dwelling taxa such as Blattodea, Scorpiones and Thysanura were present in very low abundances and species richness. Also, the number of species of Isoptera, Solifugae and Collembola were very low. This low abundances and species

richness are possibly an artefact of sampling technique used. Pitfall traps are known to have different capture efficiencies and catch results may be influenced by several factors such as trap position, the surrounding microclimate, species concerned and their body size, hunger and speed of movement (Honêk 1988; Perner & Schueler 2004).

The total species richness was highest in summer while seasonal changes in Formicidae species richness, just like their abundances showed a trough in winter. The low number of species in winter, just as the case with the number of individuals, and thei peaks in summer are generally temperature dependent, as ground-dwelling invertebrate growth rates and adult reproductivity are influenced by temperature (Andersen 1986; Wolda 1988). Overwintering (Noordhuis *et al*. 2001; Nielsen & Nielsen 2004) is another possible factor that leads to trough in species richness during winter season. Besides temperature-dependant patterns in species richness, biotic factors such as predator/ parasitoid presence and food availability also play a major role (Wolda 1988). Increased Coleoptera richness in spring could be a result of combined effects of rainfall and temperature that resulted in increased food resources. Plant productivity, composition and diversity may influence the diversity of invertebrate (Siemann 1998), and increased annual plant cover in spring could have increased food sources for herbivorous Coleoptera species, causing an increase in their species richness.

The overall Shannon species diversity and Shannon species evenness did not differ across seasons. One drawback of using Shannon diversity index is that it assumes species are randomly sampled from an infinitely large population represented by samples in which all species are represented (Pielou 1975; Magurran 1988). This estimation can therefore be affected by sampling techniques used.

This non-parametric index failed to detect differences in the evergreen and Shola forests of the Western Ghats, India (Anu & Sabu 2006). Thus, despite the differences in vegetation and weather conditions during the different seasons which affected species richness and abundances, differences could not be detected in diversity and evenness. Shannon species evenness, which also takes into account of Shannon diversity and the

maximum diversity if all species were equally abundant (Magurran 1988), was not only similar across seasons, but also low, implying that certain species were highly abundant compared to other species. Formicidae abundances were very high compared to abundances of taxa such as Blattodea and Collembola.

3.4.2 Land use effects
Species richness and abundance

In autumn, richness was significantly lower in cultivated sites compared to the other sites, while in winter the cultivated sites had significantly lower richness compared to lightly grazed sites. Formicidae were the most abundant taxa across all land uses, and together with Araneae they were more abundant in cultivated sites. However, the number of Araneae species was highest in lightly grazed sites. (Hemerik & Brussaard 2002) also found abundances of Araneae to vary in areas at different succession stage following agricultural activities. Netshilaphala *et al*. (2005) also found Formicidae species to dominate the disturbed mining sites.

Structurally diverse habitats have led to high abundances and species richness of ground-dwelling invertebrates (Andersen 1986; Greenslade & Halliday 1983; Lawrence & Wise 2004). Vegetation structure influences assemblages of Araneae by altering the nesting sites and the microclimatic conditions (Griffin 1998). The increased richness of Araneae is due to change in vegetation cover in lightly grazed sites. These sites had dwarf and large succulent plants, large non succulents and the highest plant species richness. An increase in spider richness with increasing plant architecture was found by Gibson *et al*. (1992). In Australia, Harris *et al*. (2003) found no differences in total abundance of spiders between grazed and ungrazed sites. However, there were strong correlations between percentage cover of herbs and litters and spider abundances. In our study, Tenebrionidae had the highest richness in grazed sites, with these being significantly different from cultivated sites. Though the results were not significant between land uses, the abundance of Tenebrionidae also followed the same pattern. These beetles are scavengers, feeding on plant or animal remains and their abundances are known to

increase with increasing desertification (Cloudsley-Thompson 2001), hence the grazed sites should have provided plant detritus. In the Karoo, detritivores including Tenebriondae are the major components of the diet of other invertebrate predators, including spiders (Louw & Seely 1982), therefore food availability could be one other reason for increased species richness of spiders in lightly grazed areas, where Tenebrionidae richness was also high.

Ant assemblages are influenced by the availability of habitat nesting sites, litter coverage, availability of food supply and changes in the surrounding microclimate (Greenslade 1971; Greenslade & Halliday 1983). Open habitats change the insolation of the ground and hence increased activity of ants (Hemerik & Brussaard 2002). In this study, the cultivated sites were mostly bare. High ant abundances were therefore a result of increased bare area with the resultant increased activity in these sites. *A. steingroeveri*, *O. barbiger*, *T. quadrispinosum* and *Tetramorium* sp.1 were found in high abundances in cultivated sites. *T. solidum*, *Camponotus* sp. 4, *Pheidole* sp.1 and *Monomorium* species were dominant in heavily grazed sites. Dean & Milton (1995) also found *Monomorium* sp, *Camponotus* sp and *A. steingroeveri* to be associated with recently cultivated fields and regarded these species as disturbance specialists while Andersen (1986) refers to them as opportunistic species. *A. steingroeveri* was highly dominant in the cultivated sites, though the results were not significantly different from the other sites. However, abundances for this species were ten to twenty- fold more in cultivated compared to the grazed sites. This species was the most dominant throughout the study. It is known to be widespread and a major contributor to specimens trapped in pitfalls (Boonzaaier 2006). It is a predacious scavenger which has been found in the Succulent Karoo to be very dominant in disturbed sites (Dean & Milton 1995; Netshilaphala *et al*. 2005; Tshiguvho *et al*. 1999) and in the Cape Floristic Region (Boonzaaier 2006). Ant species are known to differ in their temperature tolerances and their temperature dependent activities (Witt & Giliomee 1999). Species of *Ocymyrmex* and *Anoplolepis* have very high temperature tolerances and their foraging activity can be sustained at temperatures above 50ºC (Witt & Giliomee 1999), hence increased abundances of *A. steingroeveri* and *Ocymyrmex*

barbiger in cultivated areas was a result of increased soil surface temperatures, especially during summer months.

The myrmecines in the genus *Tetramorium* which are common gramnivores and scavengers in the Succulent Karoo (Seymour & Dean 1999; Tshiguvho *et al*. 1999) were also found to be dominant in the rehabilitated sites in the Succulent Karoo (Netshilaphala *et al*. 2005). On the other hand the other members of myrmicines; *Camponotus* sp.4 were trapped significantly more in heavily grazed compared to the other sites in autumn and in summer, *Pheidole* sp.1 and *T. solidum* were significantly more trapped in these sites compared to the cultivated and lightly grazed sites in summer. *Monomorium* species were also generally abundant in heavily grazed sites. *A. steingroeveri*, *Tetramorium* sp.1 and *T. quadrispinosum* were the most dominant in cultivated sites than in heavily grazed sites. These taxa, together with members of *Pheidole* species are known to be seed harvesters (Andersen 1986; Botes *et al*. 2006). The heavily grazed and cultivated sites had a cover of annual palnts in winter and spring. These potentially increased the seed availability after flowering in late winter-spring, favouring assemblages that are seed harvesters in these sites.

Andersen (1983) argues that although food availability controls abundances of epigaeic fauna in a broad sense, the changes in individual species could be a result of competition which has been shown to play a major role in coexistence of species. These species which are found in large numbers in degraded areas in this study could, besides food preferences, be those that favour areas where there is less competition (Dean & Milton 1995; Tshiguvho *et al*. (1999). Andersen (2000) also indicated that certain *Tetramorium* species are influenced by presence of other species and tend to prefer habitats with less competition. Thus in the present study, high abundances of *O. barbiger* and *T. quadrispinosum* in cultivated sites were a result of less competition in those sites.

Species such as *Tetramorium dichroum* (Hymenoptera: Formicidae), *Camponotus* sp.7 and *Leptothorax* sp.1 were only found in the lightly grazed sites while *Pachycondyla hottentota* was never recorded in cultivated sites. Samways (1983) outlined the

physiognomy of habitats for ants in orchards and grasslands and illustrated that most species were habitat specific and species tend to show different responses to disturbance (Hoffmann & Andersen 2003). Therefore species occurring only in lightly grazed sites could be those with specific habitat preferences. The lightly grazed sites had a high cover of succulent plants with less bare area compared to cultivated and heavily grazed sites. In general, the cultivated and heavily grazed sites are predominated by high abundances of predators and myrmecochorous, disturbance-tolerant species, and these species have the highest abundances in cultivated sites where disturbance can be regarded as highest. However, in general, species richness is high in the lightly grazed sites, though this varies significantly between seasons.

Species assemblages and indicators

The assemblage structures were significantly different across seasons for the land use types, except for winter. The cultivated and lightly grazed sites had the highest dissimilarities throughout the seasons, with the exception once again of the winter season. Winter was also the only season where variance explained by all canonical axes in the species-environment RDA did not explain the significant assemblage results. Of the three land uses, the ground-dwelling invertebrate communities of the cultivated fields were more distinct in terms of structure. A high abundance of disturbance specialists such as *A. steingroeveri* and *Tetramorium* species and predator species such as spiders constituted assemblages in these sites. Seymour & Dean (1999) also found the same results during the spring sampling done at heavily grazed and lightly grazed sites. Lindsey & Skinner (2001) also found high abundances of ants in less structurally diverse grassland areas.

The vegetation in lightly grazed sites was structurally complex. These sites had dwarf and large succulents, very large non succulent perennials and highest plant species richness. They were also rocky with less bare ground. The heavily grazed sites were comparable to lightly grazed sites in terms of rockiness and species richness. However, these sites had low cover of succulents, low cover of non succulents greater than 25 cm but high cover of dwarf non succulent perennials compared to lightly grazed. The cultivated sites were

characterised by bare ground, lowest plant species richness and predominated by highest cover of non-succulents less than 25 cm in height. There was almost a negligible cover of rocks and succulents. Seasonal vegetation composition changes were highest in these sites, together with the heavily grazed sites, with annuals contributing most of the cover in winter and spring.. The assemblages in the grazed sites were dominated by a large number of Araneae, some Tenebrionidae species and Formicidae species, while assemblages in cultivated sites were mainly Formicidae species. The assemblages in these sites were influenced by succulent plant species, rockiness and grasses. The vegetation variables explained a significant portion of the variation in ground-dwelling assemblages in autumn and spring, but not in summer and winter. Thus during the latter two seasons, extreme temperatures could have played a major role than vegetation variables in structuring assemblages. Extremely temperatures are known to slow down activity of ground-dwelling predatory insects (Maudsley *et al*. 2002). Vegetation architecture on the one hand is known to shape ground-dwelling invertebrate assemblages by altering food availability and available microhabitats (Andersen 1997; Maudsley *et al*. 2002; Donovan *et al*. 2007). Vegetation architecture is known to be significant for Araneae, with a high vegetation complexity particularly important for web-building Araneae and that shelter from wind is an important factor influencing assemblage patterns of Araneae in structurally complex vegetation (Maudsley *et al*. 2002). Assemblages in cultivated sites were influenced by bare ground, and non-succulent perennials, with Formicidae forming the major component in assemblages. Some species of Hodotermitidae and Collembola, though very few, were found in spring.

Cluster Dendograms revealed that except for autumn, ground-dwelling assemblages were dominated by species from similar study location (Kuile and Kleinfontein). This suggests that despite the clear differences between land use types, localities still play a role in determining assemblages. This was also found by Seymour & Dean (1999), where samples were dominated by similarity in location, then by land use type. The one kilometer distance between the land use types obtained in Kuile could not be met in Kleinfontein due to topographic constraints, but a minimum distance of 150m (Seymour & Dean 1999) that was found to avoid the spillover effects was far exceeded. Maudsley

et al. (2002) found spatial distributions of Coleoptera: Carabidae, Coleoptera: Staphylinidae and Arachnida: Araneae to be influenced by variability in vegetation composition and overwintering sites, showing specific habitat needs that differ for species (Samways 1983). This spatial variation has also been observed in lotic systems (Céréghino *et al*. 2001), where geographical longitude was one major driving factor, while n the Cape Floristic Region, altitude and soil type also played a major role in determining Formicidae assemblages (Botes *et al*. 2006). Spatial differences in assemblages have been attributed to factors such as competition (Lindsley & Skinner 2001) and association patterns of species feeding guilds (Donovan *et al*. 2007). Therefore factors controlling species assemblages in Kleinfontein and Kuile differ, besides the land use effects.

Three species, namely *A. steingroeveri, Tetramorium* sp.1, and *T. quadrispinosum* which were indicators for the cultivated sites were also found to be the major contributors of dissimilarity between these sites and the grazed sites. *M. capensis, Pheidole* sp.1, *T. solidum*, *Camponotus* sp.4, *Monomorium* sp.2 and Araneae sp.42 were indicators for the heavily grazed sites and only *Monomorium* sp.2 contributed to the dissimilarity between the heavily grazed sites and the other land uses. Araneae sp. 94, *Crematogaster* sp. 1, *M. capensis* and Araneae sp. 34 were indicators for lightly grazed sites and *Crematogaster* sp. 1 together with Araneae sp. 34 contributed to the dissimilarity between the lightly grazed sites and the other land uses. Botes *et al*. (2006) determined Formicidae species indicators for the Succulent Karoo, without looking into the land use effects. The authors found similar results as in the present study, where two species of *Tetramorium*, including *T. quadrispinosum*, *Pheidole* species, *Messor* species, Monomorium species and *Ocymyrmex* species were characteristic of Succulent Karoo vegetation type. In disturbed mining areas in the Succulent Karoo, *A. steingroeveri*, *Tetramorium* spp., and *Monomorium* sp. were numerically abundant compared to natural vegetation areas (Netshilaphala *et al*. 2005). Araneae have not been implicated as indicators of land use in the Succulent Karoo, while in western England, these were found to be one of the major indicator taxa for pet bogs

In conclusion, the ground-dwelling invertebrates in the Succulent Karoo reached overall abundance and species richness peaks during the hotter seasons and a trough in winter. Relative abundances and species richness for the different taxa differed between seasons. However, climatic factors significantly explained assemblage patterns in spring and not in other seasons. Vegetation changes were also more pronounced in spring, where percentage cover of annual plant was high in the cultivated and heavily grazed sites. These factors could help explain the increase in Formicidae species richness and increased abundances of Solifugae, Carabidae and Collembola. Vegetation changes explained variation in species assemblages in the different land use types except in winter. However, very few taxa respond to land use effects as opposed to seasonal changes. Tenebrionidae and Araneae are the only taxa whose species richness were affected by land use type, with vegetation structure playing a major role. Formicidae were the major contributors to assemblages in cultivated sites. Conversely, Araneae, Tenebrionidae together with Formicidae contributed to assemblages in grazed sites. Resultantly, Formicidae was the only taxon whose members were indicators for the cultivated and heavily grazed sites, while members of Araneae species were indicators, associated with lightly grazed sites. Despite the land use effects, location played a role in structuring the assemblages as was determined by cluster analysis.

3.5 Implications for management.

The low plant cover and richness and reduced structural diversity in cultivated sites may result in fewer herbivores and the concomitant reduction in carnivorous species. Tenebrionidae species richness was lowest in cultivated sites, while these sites, together with heavily grazed sites, saw a further decline in Araneae species richness. Thus the predator-prey mechanism are likely to be severely altered and as a result of cultivation and heavy grazing, diet switches may occur and assemblages may be dominated by such guilds as omnivory (Dean & Milton 1999). Increased abundances of seed harvesting Formicidae could also compound the problem. These ants harvest and store seeds of various plant species (Dean & Milton 1993; Milton & Dean 1993; Dean & Yeaton 1992). Seed harvesting ants store the most abundant seeds that they can find (Dean & Milton

1993). In heavily grazed and cultivated areas, these are likely to store seeds of annual plants and the unpalatable plant species found in these areas and hence reduced recruitment potential for perennial plant species. For instance, harvester ants, *Messor capensis* (Hymenoptera: Formicidae) nests occur at higher densities where shrubland has been degraded because of greater availability of seed of toxic shrubs and ephemeral forbs (Milton & Dean 1993). As seed mound created by harvester ants have higher soil nitrogen, phosphorus and potassium (Dean & Yeaton 1992; Dean & Milton 1993), plant recruitment in cultivated and heavily grazed sites could therefore favour certain plant species.

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Appendix A

Ground-dwelling invertebrates caught in pitfall traps and their total abundances across seasons and land use types.

		Summer			Autumn			Winter			Spring		
Taxa	**Abrev**	**CL**	**HG**	**LG**	**CL**	**HG**	**LG**	**CL**	**HG**	**LG**	**CL**	**HG**	**LG**
Arachnida: Araneae													
Araneae sp.1	Ara1											1	
Araneae sp.2	Ara2			1								2	1
Araneae sp.3	Ara3											1	
Araneae sp.4	Ara4											10	
Araneae sp.5	Ara5											1	
Araneae sp.6	Ara6											1	
Araneae sp.7	Ara7											1	3
Araneae sp.8	Ara8												2
Araneae sp.9	Ara9												2
Araneae sp.10	Ara10												1
Araneae sp.11	Ara11												1
Araneae sp.12	Ara12												1
Araneae sp.13	Ara13												1
Araneae sp.14	Ara14												1
Araneae sp.15	Ara15												1
Araneae sp.16	Ara16						1						
Araneae sp.17	Ara17					2							
Araneae sp.18	Ara18				1		3						
Araneae sp.19	Ara19						1						
Araneae sp.20	Ara20						1						
Araneae sp.21	Ara21					1							
Araneae sp.22	Ara22						4						
Araneae sp.23	Ara23						1						2
Araneae sp.24	Ara24				1		2						
Araneae sp.25	Ara25					1							
Araneae sp.26	Ara26					1							
Araneae sp.27	Ara27						1						

Species	Code												
Araneae sp.28	Ara28						2						
Araneae sp.29	Ara29					1							
Araneae sp.30	Ara30				1	2	2				2	2	
Araneae sp.31	Ara31				1		2					1	
Araneae sp.32	Ara32				1								
Araneae sp.33	Ara33					3	1						
Araneae sp.34	Ara34			1		2	1			6			1
Araneae sp.35	Ara35					5							
Araneae sp.36	Ara36	2		9		2	1				2		8
Araneae sp.37	Ara37					2	3						
Araneae sp.38	Ara38					1	2			1			
Araneae sp.39	Ara39					1							
Araneae sp.40	Ara40	2	4	5		1							
Araneae sp.41	Ara41						2					1	
Araneae sp.42	Ara42		1				1				1	8	2
Araneae sp.43	Ara43						3						
Araneae sp.44	Ara44	4	2	2			5	2	1				2
Araneae sp.45	Ara45						1						
Araneae sp.46	Ara46						1						1
Araneae sp.47	Ara47									1			
Araneae sp.48	Ara48			2				1	2	3			
Araneae sp.49	Ara49							3	1				
Araneae sp.50	Ara50							1					
Araneae sp.51	Ara51							1					
Araneae sp.52	Ara52								1	1	1	1	
Araneae sp.53	Ara53		1	8					1	2		1	
Araneae sp.54	Ara54							1					
Araneae sp.55	Ara55							1	1				
Araneae sp.56	Ara56							1					
Araneae sp.57	Ara57							1		1			
Araneae sp.58	Ara58							1					
Araneae sp.59	Ara59							1			1		
Araneae sp.60	Ara60							1					

Species	Code										
Araneae sp.61	Ara61						1				
Araneae sp.62	Ara62						1				1
Araneae sp.63	Ara63						1	1			
Araneae sp.64	Ara64						1		1	1	
Araneae sp.65	Ara65						2	3			
Araneae sp.66	Ara66						7	4	3		1
Araneae sp.67	Ara67		1				1				
Araneae sp.68	Ara68							3		1	1
Araneae sp.69	Ara69	8	2	3				5	1	1	
Araneae sp.70	Ara70							2			
Araneae sp.71	Ara71							4	1	1	1
Araneae sp.72	Ara72							1			
Araneae sp.73	Ara73							1			
Araneae sp.74	Ara74							1			
Araneae sp.75	Ara75							1			
Araneae sp.76	Ara76							1		2	5
Araneae sp.77	Ara77	4	1	10	17	18					4
Araneae sp.78	Ara78								5	6	2
Araneae sp.79	Ara79								1		
Araneae sp.80	Ara80								3		
Araneae sp.81	Ara81								1		1
Araneae sp.82	Ara82									1	
Araneae sp.83	Ara83									1	
Araneae sp.84	Ara84	1		1							
Araneae sp.85	Ara85		1								
Araneae sp.86	Ara86		1								
Araneae sp.87	Ara87	1		4							
Araneae sp.88	Ara88			1							
Araneae sp.89	Ara89			1							
Araneae sp.90	Ara90		1								
Araneae sp.91	Ara91			5							
Araneae sp.92	Ara92	1		2							
Araneae sp.93	Ara93		2	1							

Taxon	Code												
Araneae sp.94	Ara94		2	9									
Araneae sp.95	Ara95		1										
Araneae sp.96	Ara96			1									
Araneae sp.97	Ara97		1	1									
Total abundance: Araneae		**26**	**18**	**67**	**5**	**42**	**59**	**8**	**26**	**42**	**24**	**46**	**46**
Insecta: Blattodea													
Blattellidae sp.1	Bla1			1									
Blattellidae sp.2	Bla2		4										
Blattellidae sp.3	Bla3		2	3									
Blattellidae sp.4	Bla4											1	
Blattidae sp.1	Blat1												1
Total abundance: Blattodea		**0**	**6**	**4**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**
Insecta: Coleoptera													
Carabidae sp.1	Car1	3	2	2							1	8	7
Carabidae sp.2	Car2		1									2	
Carabidae sp.3	Car3												4
Carabidae sp.4	Car4								1	1			
Carabidae sp.5	Car5									1			
Carabidae sp.6	Car6										1		1
Carabidae sp.7	Car7										1	1	
Tenebrionidae sp.1	Ten1											1	
Tenebrionidae sp.2	Ten2		17									1	2
Tenebrionidae sp.3	Ten3		1				1					1	
Tenebrionidae sp.4	Ten4					1							
Tenebrionidae sp.5	Ten5					1	4					3	3
Tenebrionidae sp.6	Ten6						3		3	4	1	3	1
Tenebrionidae sp.7	Ten7					1							
Tenebrionidae sp.8	Ten8	18	63	25		14							1
Tenebrionidae sp.9	Ten9									1			
Tenebrionidae sp.10	Ten10									1			
Tenebrionidae sp.11	Ten11									2			
Tenebrionidae sp.12	Ten12										3	1	4
Total abundance: Coleoptera		**21**	**84**	**27**	**0**	**17**	**8**	**0**	**4**	**10**	**7**	**21**	**23**

Hexapoda: Collembola

Taxon	Code	1	2	3	4	5	6	7	8	9	10	11	12	13
Collembola sp.1	Coll1										15			
Collembola sp.2	Coll2									1				
Collembola sp.3	Coll3									2				
Collembola sp.4	Coll4									1				
Collembola sp.5	Coll5										1			
Insecta: Hymenoptera: Formicidae														
Formicinae														
Anoplolepis steingroeveri (Forel)	Aste	20930	1755	1059	17040	3829	1302	1106	379	754	903		1396	1615
Camponotus fulvopilosus (De Geer)	Cful	187	162	181	39	36	34	2	14	9		133	493	94
Camponotus sp.1	Cam1													1
Camponotus sp.2	Cam2					3	3	1						
Camponotus sp.3	Cam3							4	4	9		6	2	10
Camponotus sp.4	Cam4			4	1		8					3	5	
Camponotus sp.5	Cam5						1		1					
Camponotus sp.6	Cam6		17	29	16	3	21	9	6	16	5	29	30	23
Camponotus sp.7	Cam7	1		1		2	2	13						
Lepisiota sp.1	Lep1	2											2	
Lepisiota sp.2	Lep2		8	37	76	2	13	20			1		2	3
Myrmicinae														
Crematogaster sp.1	Cre1			30	24	3		188						
Crematogaster sp.2	Cre2		18	521	1049	170	48	61	49	150	1		110	48
Crematogaster sp.3	Cre3			1		1		1			1			
Leptothorax sp.1	Lept1							25						
Messor capensis (Mayr)	Mcap	4		78	5	8		18	68					
Monomorium sp.1	Mon1		58	17	93	327	290	3	32	17	47		74	18
Monomorium sp.2	Mon2		2			33	604	158		1		1	2	5
Monomorium sp.3	Mon3						5	1		3			51	2
Monomorium sp.4	Mon4		1270	2562	446	21	15	55						
Ocymyrmex barbiger (Emery)	Obar		521	202	71	50	57	5		1		11	22	12
Pheidole sp.1	Phe1			9										
Tetramorium quadrispinosum (Emery)	Tqua		239	15	30	17	12	9		1		2	2	3
Tetramorium solidum (Emery)	Tsol	1		11	2	34		25	14			10	5	2

Species	Code												
Tetramorium dichroum (Santschi)	Tdic				8	1							
Tetramorium sp.1	Tet1	723	31				21	2			445	45	12
Ponerinae													
Pachycondyla hottentota (Emery)	Phot	4	11	7		1	8		2		1	1	4
Total abundance: Formicidae		**23986**	**5475**	**3069**	**17249**	**5149**	**2253**	**1204**	**505**	**945**	**1593**	**2240**	**1854**
Insecta: Isoptera													
Hodotermitidae sp.1	Hod1		1										
Hodotermitidae sp.2	Hod2				2	8	1	1					
Hodotermitidae sp.3	Hod3	3			1		4						6
Hodotermitidae sp.4	Hod4	69	7	11		5	4		2	1	5	1	
Kalotermitidae sp.1	Kal1					2	1	1					
Kalotermitidae sp.2	Kal2		1	2			4						
Termitidae sp.1	Ter1					1	1					1	
Termitidae sp.2	Ter2	1							1		1		21
Total abundance: Isoptera		**73**	**9**	**13**	**3**	**16**	**15**	**2**	**3**	**1**	**6**	**2**	**27**
Arachnida: Scorpiones													
Scorpione sp.1	Sco1		2										
Scorpione sp.2	Sco2	2		1									
Total abundance: Scorpiones		**2**	**2**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Arachnida: Solifugae													
Solifugae sp.1	Sol1												1
Solifugae sp.2	Sol2	3	15	11		4	8		2			1	
Solifugae sp.3	Sol3		1	1									1
Solifugae sp.4	Sol4				1								
Solifugae sp.5	Sol5					1							
Solifugae sp.6	Sol6		3				2						
Solifugae sp.7	Sol7				1								
Solifugae sp.8	Sol8		1										
Solifugae sp.9	Sol9	1	5	5									
Solifugae sp.10	Sol10		1										
Solifugae sp.11	Sol11	2		1									
Solifugae sp.12	Sol12	1	23	38									
Total abundance: Solifugae		**7**	**49**	**56**	**2**	**5**	**10**	**0**	**2**	**0**	**0**	**1**	**2**

Insecta: Thysanura

Lepismatidae sp.1	Lepi1	1											
Total abundance: Thysanura		**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Overall abundances		**24115**	**5644**	**3237**	**17259**	**5229**	**2345**	**1214**	**540**	**998**	**1630**	**2311**	**1953**

CHAPTER 4. RESPONSES OF FLYING INSECTS TO DIFFERENT GRAZING INTENSITIES AND CULTIVATION IN A THIRTY YEAR OLD FALLOW FIELD, IN THE SUCCULENT KAROO.

4.1 Introduction

The Succulent Karoo is well known for its high levels of floral species richness and endemism (Hilton-Taylor 1994). In comparison to other semi-arid regions, plant species richness of the Succulent Karoo is known to be exceptional (Cowling *et al*. 1999; Cowling & Hilton-Taylor 1999). Invertebrates, though less recognised, form the greater part of the fauna (Struck 1994a, b). Many higher trophic level invertebrate taxa are well represented (Picker & Midgley 1996; Struck 1994c; Goldblatt *et al*. 1998), especially for pollinators which display high levels of adaptive radiation and associations with the flora (Colville 2006). The high species richness and unique global status of the Succulent Karoo requires urgent conservation as land use practices continue to threaten the area (Lombard *et al*. 1999).

Habitat transformation through anthropogenic effects presents a single most important threat to global biodiversity (Wessel *et al*. 2000). For instance, up to 25% of South Africa's natural land cover has been estimated to have been converted to other forms of land use such as agriculture (Macdonald 1989). The Succulent Karoo is no exception to this conversion of natural habitats due to human land use. Agricultural fields, both intensive and extensive as well as irrigation schemes have been established along most perennial rivers (Hilton-Taylor & Le Roux 1989). There is also extensive dry-land cultivation in some parts of the Succulent Karoo and this leads usually to abandoned lands due to the unpredictability of rainfall (Hilton-Taylor & Le Roux 1989; Allsopp 1999). The abandoned lands may take years to revert to their original state. If cultivated fields are abandoned, a succession of different vegetation types with associated faunas occurs (Erhardt 1985; Dean & Milton 1995). Heavy grazing of rangelands has also placed biodiversity of these areas at risk (Simons & Allsopp 2007), mainly due to the associated vegetation changes (Todd & Hoffman 1999; Todd & Hoffman 2000).

Research in the Succulent Karoo has focused mainly on plants, and very little on invertebrates (Milton & Dean 1992; Struck 1994a, b; Picker and Midgley 1996; Seymour & Dean 1999; Mayer 2004, Mayer 2005; Gebeyehu & Samways 2006a, b and Mayer *et al*. 2006). This extended research on vegetation has enabled models to be put forward on interactions of climate change and land use (mainly grazing) and vegetation (Hahn *et al*. 2005; Richardson *et al*. 2005; Richardson & Hahn in press a, b). None such models exist for invertebrates, despite their importance in ecosystem functions, such as in pollination of this unique flora of the area (Struck 1994a, b, c; Picker & Midgley 1996; Mayer *et al*. 2006).

Vegetation patterns are the major determinants of invertebrate assemblages, mainly through their composition and architecture (Kevan & Baker 1999; Gebeyehu & Samways 2006a, b). Vegetation acts both directly and indirectly in determining invertebrate assemblages. It directly provides feeding sites, mating sites, egg-laying and refugia for invertebrates (Opp & Prokopy 1986; Gebeyehu & Samways 2006a) and the quality of these resources is essential in habitat selection. Vegetation cover alters humidity, air temperature, soil temperature and moisture, wind speed and light intensity, thereby creating a range of microclimates that provide several niches for a wide range of invertebrate species (Edwards & Wratten 1980). Habitat destruction therefore leads to destruction of these resources (Kevan & Baker 1999) and niches, and this can lead to a cascading effect to other trophic levels (Kevan & Baker 1999). It is therefore highly essential to gain fundamental knowledge of processes that characterise assemblages of invertebrates in areas of different land use (Butt *et al*. 1980; Kishbaugh & Yocon 2000; Pinheiro *et al*. 2002).

The aim of this study was therefore to determine how light grazing, heavy grazing and previous cultivation of fodder crops in a field that has been left fallow for 30 years affect the assemblages of flying invertebrates by addressing the following questions:

1. Is there any difference in terms of abundance, species richness, diversity and evenness of flying invertebrates in the three land use types across seasons and within seasons, more especially with regard to pollinator taxa, as identified by Struck (1994a, b)?

2. Do the observed weather and vegetation/habitat changes explain changes in flying invertebrate assemblages across land use types and seasons?

3. Are there certain groups of invertebrates that can be regarded as indicators for land use during the four seasons?

4. What are implications of the findings for the conservation of flying invertebrates in the Succulent Karoo?

4.2 Material and methods

4.2.1 Study area and sampling design

The study was undertaken in Paulshoek area (30°20′S; 18°14′E) in the Leliefontein district of Central Namaqualand, Northern Cape. The area is part of the winter rainfall Succulent Karoo of South Africa (Todd & Hoffman 1999). Paulshoek receives an average of 180mm of rainfall per year, with much variation between years (Simons 2005). The area falls within the Namaqualand Hardveld bioregion (Mucina *et al*. 2006), and is dominated by members of the families Asteraceae, Mesembryanthemaceae, Crassulaceae and Aizoaceae (Petersen 2004), with the lowland areas of Paulshoek dominated by *Galenia africana* L. (Aizoaceae) and *Ruschia robusta* L. Bolus (Mesembryanthemaceae) (Todd & Hoffman 1999). Surface soils are sandy with over 50% of the grains having a diameter of greater than 0.3mm (Allsopp 1999).

Livestock farming and cultivation of fodder crops are the two main agricultural activities of the area. In Paulshoek, livestock farming is based on communal land tenure system, affording all inhabitants access to rangelands (May 1997). However, for the past 30 years, the stocking rate in Paulshoek has been twice that recommended by the Department of Agriculture (Todd & Hoffman 1999). The resultant effects of browsing by sheep, goats and donkeys are evident, especially around the stock posts (Simons 2005). In comparison to these communally owned rangelands, the neighbouring privately owned farms have been kept at recommended stocking rates and therefore lightly grazed.

Cultivation of oats, wheat, rye and barley depends on rainfall and availability of resources (Allsopp 1999). In most cases, fields may be left fallow for several years without cultivation (Allsopp 1999), and successional change of vegetation usually results.

Two localities in the Paulshoek area were chosen for the study; Kuile and Kleinfontein (see Figure 3.1, chapter 3). The continuously high stocking rates on communal rangelands in Kuile and Kleinfontein resulted in a clear fence line contrast between the communal rangelands and the neighbouring commercial farms (see Figure 3.2, chapter 3). In Kleinfontein, fodder crops were cultivated in 1977. Thirty years after abandonment, the vegetation of the fallow field is now dominated by *Galenia africana* L. and characterised by resprouting of annuals after the winter rains.

Three plots per land use type were chosen for the study. The 30 year old fallow field is for simplicity referred to as cultivated field throughout the text. Two heavily grazed plots and two lightly grazed plots were selected at Kuile communal site and commercial site respectively. The third plots for the heavily grazed and lightly grazed sites were at Kleinfontein communal and commercial sides of the fence. All three cultivated field plots were located in Kleinfontein (see Figure 3.2, chapter 3). No pristine plots were investigated to allow the determination of which land use type had the least impact. This is because there are no pristine areas under conservation located in this area. Within each plot, three trapping arrays (Figure 4.1) were set up, approximately 150 m apart. In Kuile, arrays were set at least 1 km from the fence, but this could not be achieved in Kleinfontein due to topographic constraints. However, a distance of at least 150 m was kept between land use types to avoid spilling over effects (Seymour & Dean 1999). In each array, six differently coloured pan traps were used to capture the flying invertebrates. Colours selected were red, orange, yellow, white, blue and purple (Figure 4.1). This is because insects are known to belong to different colour guilds (Picker & Midgley 1996; Colville *et al.* 2002; Mayer *et al.* 2006), which range from 300nm (ultraviolet) to 650nm (yellow-orange) (Kevan & Baker 1983). Using the differently coloured traps thus ensured that insects belonging to all colour guilds were captured.

Flying insects were collected in plastic pan traps (11.5 cm diameter and 5 cm depth) painted with high gloss enamel paints of the colours red, orange, mid chrome yellow, white, blue and lilac (purple), manufactured by SPECTRE Coatings Company. The pan traps were three quarter filled with water in which a few drops of liquid detergent were added to break the surface tension. A set of six pan traps were placed 25 cm from the centre of the pitfall cross. These were placed circularly on the ground in a rainbow arrangement; red, orange, yellow, white, blue and lilac (purple) around the cross-array of pitfall traps (Figure 4.1, see also chapter 3). The red and orange pan traps were placed on one side of the cross, with 20 m distance between them and so were the blue and white traps, which were opposite the red and orange, also with 20 m distance between. The purple and yellow traps were in the middle of the last two sides of the pitfall cross, opposite each other (Figure 4.1). The pan traps were placed on the ground, as the vegetation on all sites was fairly low and open and it was thus not required to raise the traps above the vegetation. The insects fly readily into the coloured traps and are unable to escape once wet (Colville *et al*. 2002).

Specimens were removed from the traps with narrow-tipped featherweight forceps and put in labeled plastic sample bottles in which 70% ethyl alcohol has been added. Specimens from all the six pan traps were combined into a single sample for all the grids. The sample bottles were labeled according to sampling date and site.

The invertebrates were collected from the traps every twenty-four hours with forceps for a period of seven consecutive days for all four sampling seasons. The water was replaced after collections if it had dropped below half the trap capacity. They were then sorted into recognisable taxonomic units (RTUs) and counted under a dissecting microscope in the laboratory. The RTUs were then identified using keys in Scholtz & Holm (1986). Those which could not be identified were sent to Professor Henk Geertsema, Department of Conservation Ecology and Entomology, University of Stellenbosch. Voucher specimens are kept at the Entomology museum, University of Stellenbosch. Specimens were identified mostly to family level and where (further) identification was not possible, these were assigned to (RTUs)/ morphospecies codes.

The first sampling was done in March 2006 for autumn season; the second sampling was done in July 2006 in the winter season. The third and fourth samplings were done in September 2006 and January 2007 for spring and summer seasons respectively. The positions of the grids were marked with a Garmin GPS during the first sampling, so that the same grids could be used for the subsequent seasonal samplings. The same sampling procedure was repeated during the four sampling seasons.
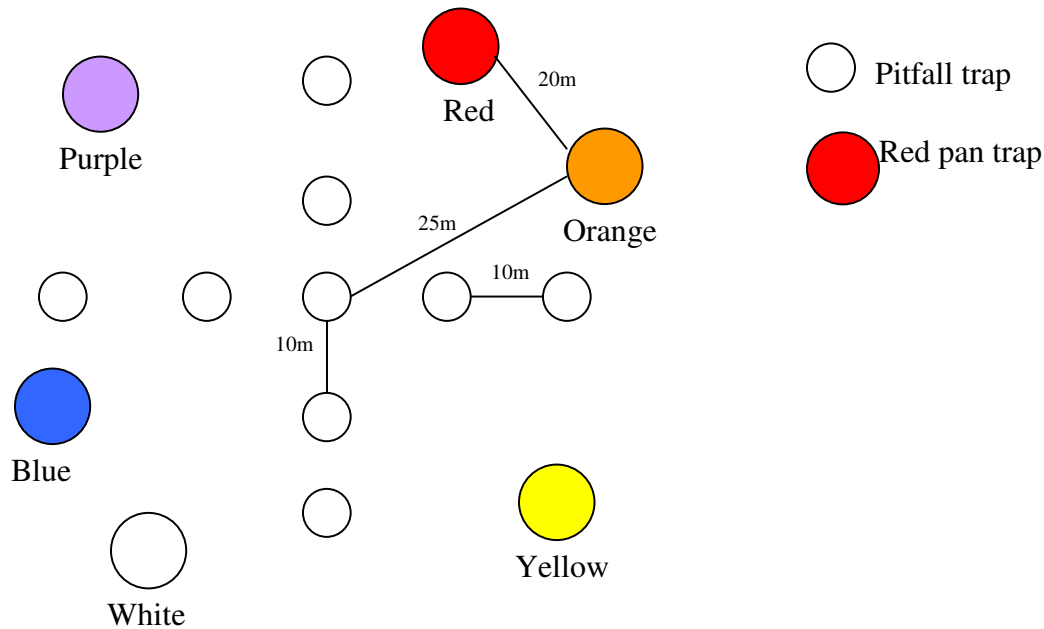
Figure 4.1. Schematic trapping array showing arrangement of pan traps (with their respective colours: red, orange, yellow, white, blue and purple) around the cross array of pitfalls at each of the sampling sites in the sampling grid. Distances are not to scale.

4.2.2 Vegetation and climatic data

For each of the sampling events, vegetation structure next to each of the pitfall grids was sampled. Vegetation surveys were carried out to determine if changes in structure and composition explain the assemblages of ground-dwelling invertebrates in the three land use types. Rock cover, bare area and plant species composition and height were recorded along a 50 m line close to the pitfall cross using the line intercept method (Milton & Dean 1992) to estimate their cover (Colville *et al*. 2002). For each of the grids, a 50 m transect was sampled once during the seven-day sampling period for every season. At

every 1 m intercept along the transect, the heights of plant species that were directly hit by the measuring tape were determined using a 5 m measuring tape. Herbarium specimens and pictures were taken for identification for plant species that could not be identified in the field. A Sony Cyber-Shot camera with 7.2 Megapixel, 3X optical Zoom lens and Carl Zeiss lens was used to take pictures. Plants were later identified at least to genus level. Growth and life form were also determined. Identification was done by Professor M.T. Hoffman, Lesley Hill Institute of Plant Conservation, University of Cape Town. Bare ground as well as rocky areas were noted along the transect. These were also hits at the 1 m intercept along the transect. This enabled the estimation of the total percentage cover, percentage cover of each plant species and cover of exposed and rocky area as hits for each category divided by the transect length and multiplied by one hundred. Plants were classified as grasses, annuals, succulent perennials and non-succulent perennials, as determined from life form and growth form. Vegetation structure was estimated by assigning different height classes to all perennials: succulent perennials greater than 25 cm, succulent perennials less than 25 cm, non-succulent perennials greater than 25 cm and non-succulent perennials less than 25 cm (Todd & Hoffman 1999). Cover for the different vegetation classes, annuals, grasses, rocks and bare ground were then estimated.

Weather data for the area were obtained from BIOTA web site. The weather station is situated at the fence between the BIOTA observatories Leliefontein 624 (Paulshoek) and Remhoogte 416 (Rooiwal) (30º 23' 41.1 ''S, 18º 17' 10.1''E). The weather data included rainfall, minimum and maximum temperatures, relative humidity of the air and minimum and maximum wind speed for the seven day sampling period.

4.2.3 Data analyses

For vegetation sampling, mean (±SD) percentage cover for each of the categories; annuals, bare area, grass, rocks, succulent perennials and non succulent perennials were determined using grid data for each of the land uses for each season. For height classes, mean (±SD) were determined. Statistical differences were determined using Mann-Whitney U-test. Mean (±SD) number of plant species was also determined for each land

use for all seasons. Statistical differences were determined using one way ANOVA for each season. Percentage covers of the two plant species that were dominant per site were also determined.

Weather data were plotted to depict their variations. Rainfall was plotted for the year in which sampling was conducted (March 2006 to January 2007). Mean (±SD) for minimum air temperature, wind speed, relative humidity of the air and solar radiation were plotted for the seven-day seasonal sampling.

Data from the sampling grid were pooled into a single sample per plot. Total abundance, diversity, species richness and species evenness of invertebrates in heavily grazed, lightly grazed and cultivated plots were determined across all seasons for all invertebrate taxa combined. Species richness is the total number of species/ RTU's present at each plot and abundance is the absolute number of individuals in each species or RTU present at each plot. Diversity was calculated using Shannon-Wiener diversity index (H) which also takes into account evenness of species abundances (Ohsawa 2005). These indices were calculated using CanoDraw in CANOCO, version 4.5 (Lepš & Šmilauer 2003). Results were tested for significant differences using factorial ANOVA with season and land use as the main effects and Bonferroni tests as post-hoc tests in STATISTICA 7 (StatSoft Inc. 2003). Relative abundances and richness were also calculated across seasons for each of the invertebrate orders within land use types (cultivated, heavily grazed, lightly grazed) and for taxa between land use types. Relative abundance is the absolute number of individuals of a species at each plot divided by the total number of individuals of all species at that plot multiplied by one hundred. Differences in relative abundances and species richness were then tested using Kruskal-Wallis ANOVA and Mann-Whitney U-test, as data were non-normally distributed.

To determine whether species were characteristic for a certain land use type, their indicator values were determined using the Indicator Value Method by Dufrêne and Legendre (1997). This method determines the indicator value (INDVAL) as a percentage for each species based on both specificity (uniqueness to a site) of a species to a land use type and its fidelity (frequency within that site). A high indicator value indicates that a

species can be regarded as being characteristic of that particular area (Botes *et al*. 2006). For this study, a subjective benchmark indicator value of above 70% was used, as species having values greater than this benchmark can be regarded as indicators (McGeoch *et al*. 2002).

To determine whether species composition of invertebrate communities differed between land use types, patterns in invertebrate composition were examined using multivariate statistical techniques. Specifically, ordination and cluster methods were used to determine patterns in species space relative to land use type. Data sets were first reduced by eliminating extremely rare species. These were species whose abundance was less than 5 individuals in total for every season (Seymour & Dean 1999). These species are removed from data analysed with multivariate techniques because their presence may be due to chance rather than due to the ecological conditions and their inclusion masks underlying patterns (Gaston 1994).

After reduction of extremely rare species, i.e. species with a abundance of less than five individuals per species, from the data, Redundancy analysis (RDA) was used to determine the relationship between the invertebrate assemblage structure and environmental and climatic variables within each season using CANOCO, version 4.5 (Lepš & Šmilauer 2003). It should be noted that exclusion of extremely rare species does not moderate for the effects of rare and abundant species in the data sample to be used for analysis (Collville *et al*. 2002). For this reason, in addition to removing extremely rare species, the abundance data were $\log_{10}$ transformed to moderate for the effects of both rare and highly abundant morphospecies (Clarke & Warwick 1994), as outlined by Collville *et al*. 2002. The significance of the variables was tested with Monte-Carlo permutation test (Lepš & Šmilauer 2003). For climatic data, a set of eight variables was used and their significance tested with Monte-Carlo permutation tests. Because of the high degree of correlation amongst these variables, only four variables; amount of rainfall, minimum temperature of the air, solar radiation and wind speed, all averaged over the sampling period, were used in the model and their significance also tested with Monte-Carlo permutation tests.

To group sites according to their similarity as determined by assemblage structure, cluster analysis was used using the statistical programme PRIMER (Plymouth Routines in Multivariate Ecological Research) v5 (Clarke & Gorley 2001). Cluster analysis was based on Bray-Curtis similarity matrices (Clarke & Warwick 2001). Abundance data were square-root transformed to down-weight rare and abundant species (Clarke & Warwick 2001). The Bray-Curtis similarity matrix was also used in an ordination plot using non-metric multidimensional scaling (MDS) to obtain stress values (Clarke & Gorley 2001). A stress function assesses how well the two-dimensional plot represents the actual sample relationship. The lower the stress value, the more accurate the representation of samples in ordination (Clarke & Warwick 2001). Analysis of similarity (ANOSIM) was used to test for significant differences between sites (Seymour & Dean 1999). One-way ANOSIM test statistic R is obtained. The null hypothesis (there are no land use differences), is rejected at 5% significance level (Clarke & Gorley 2001). Pair wise land use differences are determined by pair wise R values. An R value of 0 means that sites are indistinguishable while an R value of 1 means that sites are completely dissimilar (Clarke & Gorley 2001). Invertebrate assemblages from each land use were compared using the similarity percentage (SIMPER) programme in PRIMER to determine species responsible for differences between sites (Seymour & Dean 1999).

4.3 Results
4.3.1 Seasonal effects

Total Species richness, abundance, diversity and evenness

Excluding extremely rare taxa, a total of 23 544 flying invertebrate individuals were captured during the four sampling seasons. 4 408 individuals were sampled in summer, 7 939 in autumn, 4 081 in winter and 7 118 in spring (Appendix 1). Analysis with factorial ANOVA showed significant differences between seasons in terms of species richness and Shannon diversity indices (Table 4.1). The number of species was significantly higher in spring compared to the other three seasons ($F_{3, 24} = 57.538$, p = 0.0000, Table 4.1).

Species diversity was significantly higher in spring compared to winter and summer ($F_{3, 24}$ = 7.573, p = 0.001, Table 4.1). There was no difference in overall evenness between seasons ($F_{3, 24}$ = 2.444, p = 0.083, Table 4.1). There were no significant differences in the overall species richness $F_{(2, 24)}$ = 0.597, p = 0.558, diversity $F_{(2, 24)}$ = 0.93, p = 0.408, evenness $F_{(2, 24)}$ = 1.264, p = 0.300 and abundance $F_{(2, 24)}$ = 0.248, p = 0.782 between land use types.

Table 4.1: Mean species richness S, mean Shannon diversity index H, mean Shannon species evenness index E and mean total abundance N of all flying invertebrates caught in pan traps for the four seasons., using combined grid data. Means with different letters are statistically different within columns (p< 0.05).

Season	S ± SD	H ± SD	E ± SD	N ± SD
Summer	60.78 ± 10.13 **a**	2.54 ± 0.81**a**	0.63 ± 0.21	529.11 ± 469.38
Autumn	103.00 ± 22.96 **b**	3.06 ± 0.32 **ab**	0.66 ± 0.49	911.56 ± 386.48
Winter	49.78 ± 0.61 **a**	2.76 ± 0.33 **a**	0.71 ± 0.73	504.78 ± 213.64
Spring	138.33 ± 25.22 **c**	3.69 ± 0.88 **b**	0.75 ± 0.18	993.11 ± 796.38

Species richness and relative abundance of taxa across seasons

The Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera were the most abundant and species rich orders across the seasons (Figure 4.2A and 4.2C). Blattodea, Dermaptera, Neuroptera, Orthoptera, Psocoptera and Thysanoptera were present only in very low abundances and in low species numbers (Figure 4.2B and 4.2D). Peaks in abundances and richness differed between orders and between seasons. Coleoptera, Hymenoptera and Lepidoptera showed significant variation in relative abundance across seasons (Figure 4.2A); Coleoptera $H_{(12, 3)}$ = 9.974, p = 0.019, Hymenoptera $H_{(12, 3)}$ = 8.128 p = 0.043 and Lepidoptera $H_{(12, 3)}$ = 8.744, p = 0.033. Hymenoptera were more abundant in summer while abundance of Lepidoptera peaked in autumn. Coleoptera were more abundant in winter (Appendix 1).

Kruskal-Wallis ANOVA results showed that Diptera ($H_{(12, 3)}$ = 9.974, p = 0.019), Hymenoptera ($H_{(12, 3)}$ = 8.128, p = 0.043) and Lepidoptera ($H_{(12, 3)}$ = 8.744, p = 0.033) showed significant variation in species richness across seasons (Figure 4.2C).

Hymenoptera and Lepidoptera species richness were highest in autumn while the number of species of Diptera was highest in spring, followed by autumn (Figure 4.2C).

A
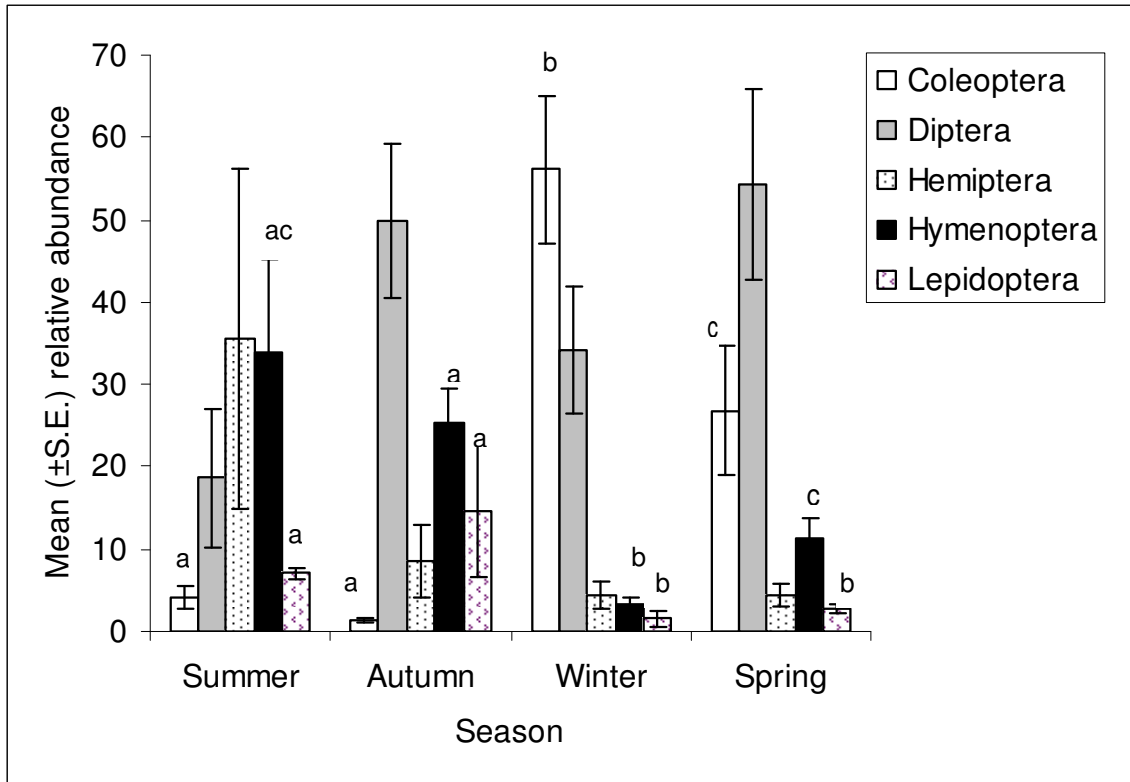
B
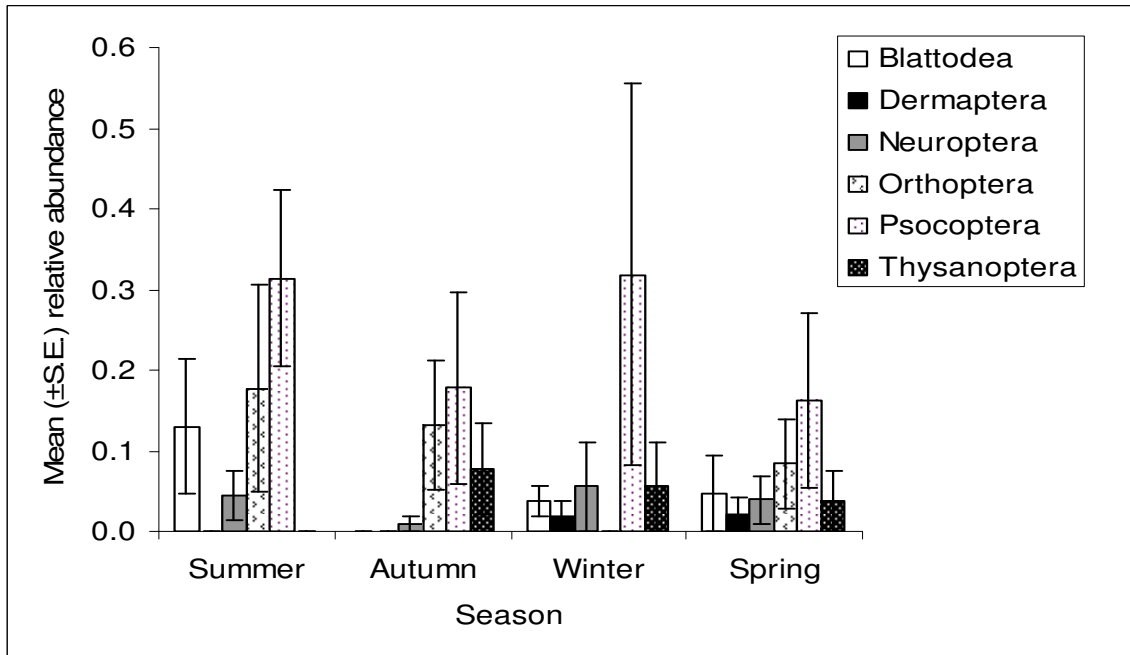
Figure 4.2:**A)** Mean (±SE) relative abundance of the most common flying insect orders caught in pan traps, **B)** the least common flying insect orders caught in pan traps, for the four different seasons sampled, using combined grid data. Orders showing significant variation within them between seasons as tested with Mann-Whitney U-test are shown with different lower case letters.

C
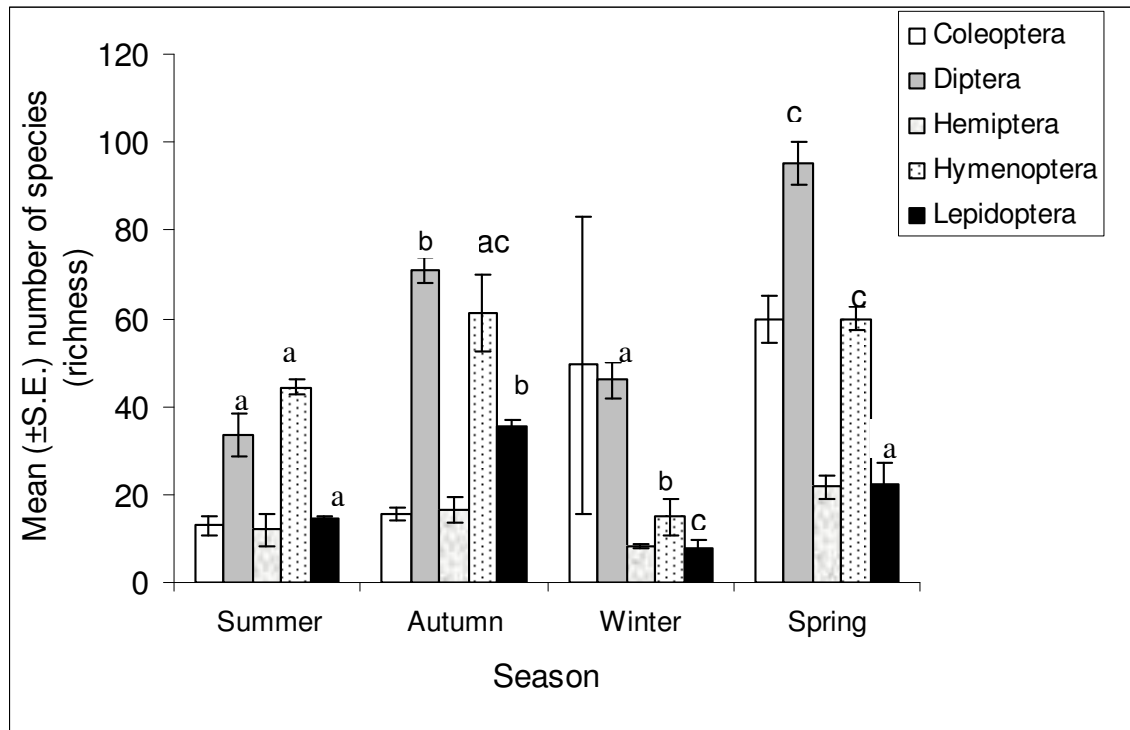
D
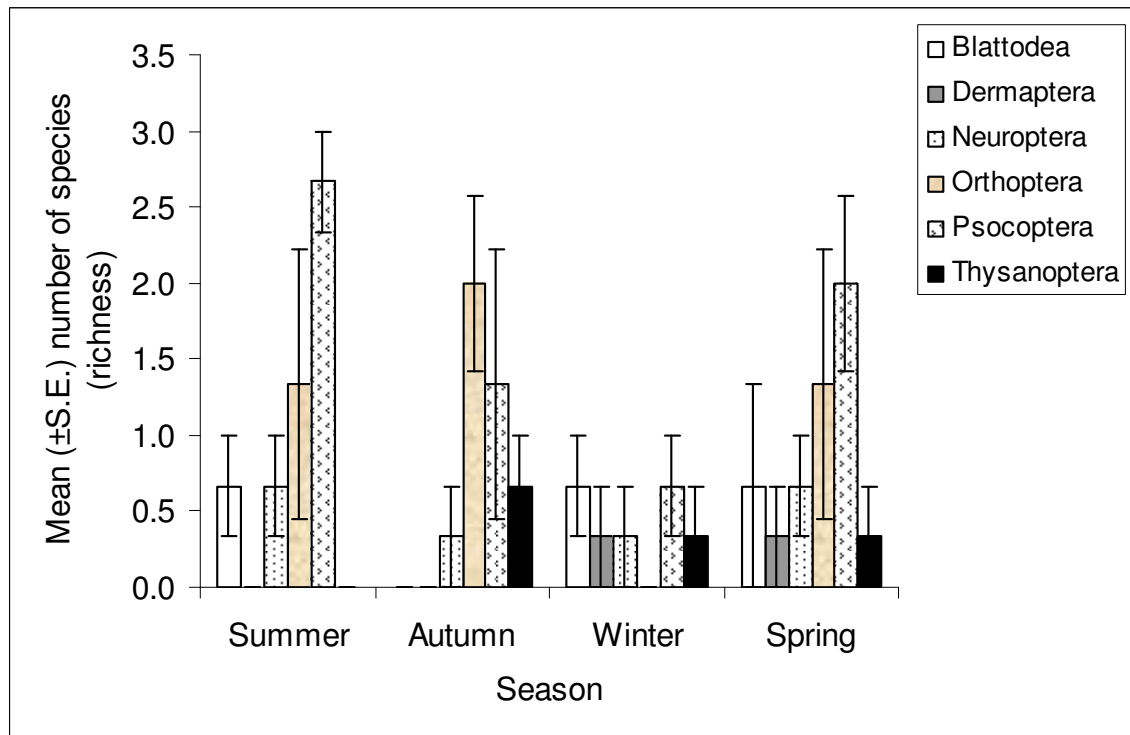
Figure 4.2:C) Mean (±SE) species richness of the most common flying insect orders caught in pan traps, **D)** the least common flying insect orders caught in pan traps, for the four different seasons sampled, using combined grid data. Orders showing significant variation within them between seasons as tested with Mann-Whitney U-test are shown with different lower case letters.

Species assemblages

Figures 4.3A, 4.3B, 4.3C and 4.3D, show RDA bi-plots of the species-climatic variables relationship for the four seasons investigated. Abbreviations for all the species are shown in Appendix 1. In summer and winter, few species were influenced by climatic variables (Figures 4.3A and 4.3C), while in autumn and spring, a large number of species showed a relationship with climatic variables (Figures 4.3B and 4.3D). Accordingly, the assemblage composition differed between seasons. The first axis represents climatic gradient of increasing wind speed and solar radiation and decreasing rainfall and air temperature. Pollinator species (Struck 1994a, b) in the families Halictidae (Hymenoptera) (Abbreviated as in Appendix 1: Hal1 and Hal8) and Curculionidae (Coleoptera) (Curc9) increase in abundance with hotter and wet conditions (Figure 4.3A). Abundances of Diptera families: Agromyzidae (Agr14), Chloropidae (Chl9) and Therevidae (The11) and two Hymenoptera pollinator families (Struck 1994a) Halictidae (Hal7) and Anthophoridae (Anth6) increase with windy and sunny conditions. In autumn, conditions were hot and windy (Figure 4.3B), and two species of pollinators (Struck 1994a, b) (Hymenoptera: Halictidae) (Hal14 and Hal18) and some microlepidoptera (Lepidoptera) (Mic41 and Mic34) favoured these conditions. Most of the other species however decreased in abundance with these hot and dry conditions. In winter, members of Halictidae (Hal20 and Hal22) and Melittidae (Hymenoptera) (Mel16 and Mel17) preferred hotter and windy conditions (Figure 4.3C) and abundances of one species of Scarabaeidae (Hopliini) (Sca10) increased with decreasing rainfall gradients. In spring, Scarabaeidae (Hopliini) (Sca21, Sca23, Sca24 and Sca27) and Hymenoptera: Sphecidae (Sph16 and Sph18) abundances increased with cooler and rainy conditions (Figure 4.3D). For all the seasons, Monte-Carlo tests show climatic variables to have significant explanatory effects on assemblages (Figure 4.3A, 4.3B, 4.3C and 4.3D).
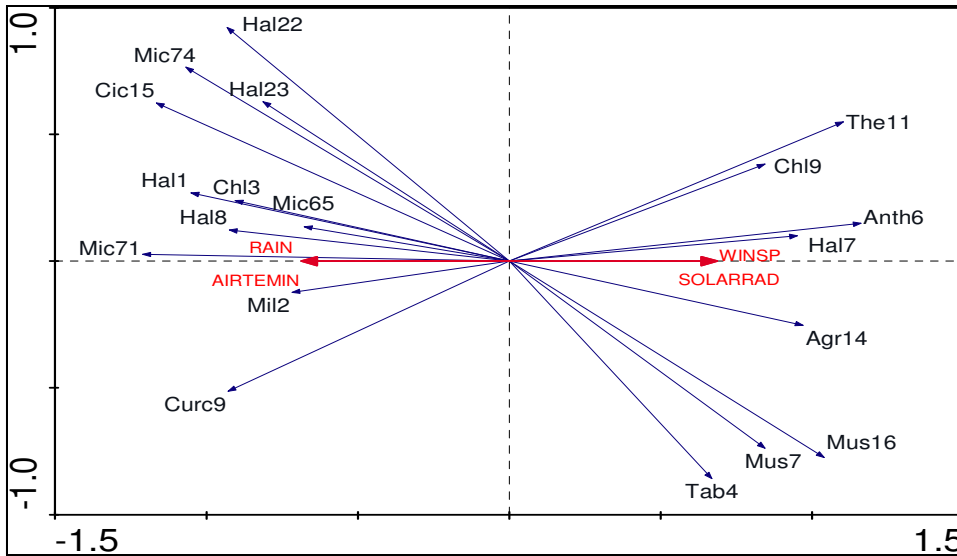
Figure 4.3A: Redundancy analysis (RDA) biplot of flying insect species caught in pan traps and climatic variables for summer, using combined grid data. Only species that have their abundances explained by the first axis are shown (abbreviations in Appendix 1). Axis 1 and 2 respectively explain 21.9% and 18.1% variance in species-environmental relation. Monte-Carlo test of significance of all canonical axes: $F = 1.965$, $p = 0.048$. Climatic variable names: RAIN= Average rainfall, AIRTEMIN= Average minimum air temperature, WINSP= Average wind speed, SOLARRAD= Average solar radiation.
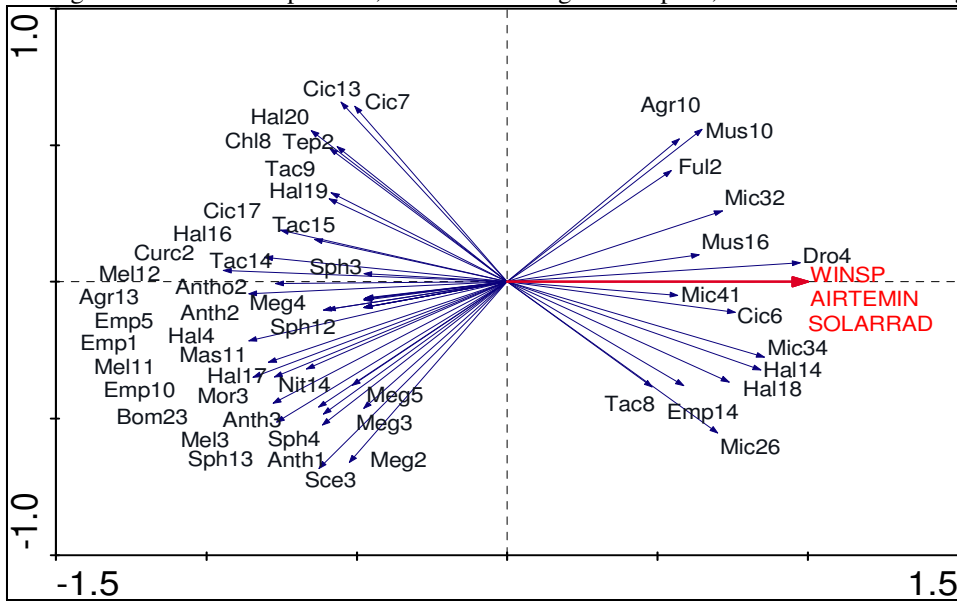
Figure 4.3B: Redundancy analysis (RDA) biplot of flying insect species caught in pan traps and climatic variables for autumn, using combined grid data. Only species that have their abundances explained by the first axis are shown (abbreviations in Appendix 1). Axis 1 and 2 respectively explain 21.9% and 19.3% variance in species-environmental relation. Monte-Carlo test of significance of all canonical axes: $F = 1.968$, $p = 0.034$. Climatic variable names: AIRTEMIN= Average minimum air temperature, WINSP= Average wind speed, SOLARRAD= Average solar radiation.
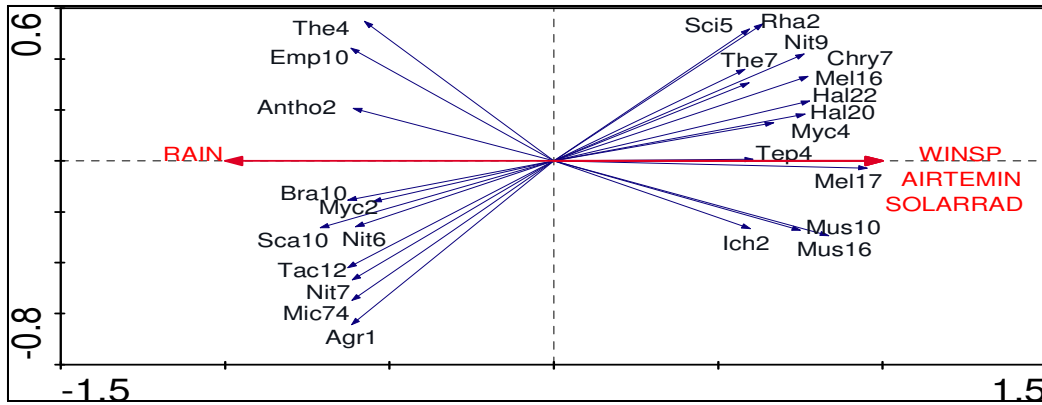
Figure 4.3C: Redundancy analysis (RDA) biplot of species and climatic variables for winter, using combined grid data. Only species that have their abundances explained by the first axis are shown (Appendix 1). Axis 1 and 2 respectively explain 28.8% and 16.5% variance in species-environmental relation. Monte-Carlo test of significance of all canonical axes: F = 2.835, p = 0.020. Climatic variable names: RAIN= Average rainfall, AIRTEMIN= Average minimum air temperature, WINSP= Average wind speed, SOLARRAD= Average solar radiation.
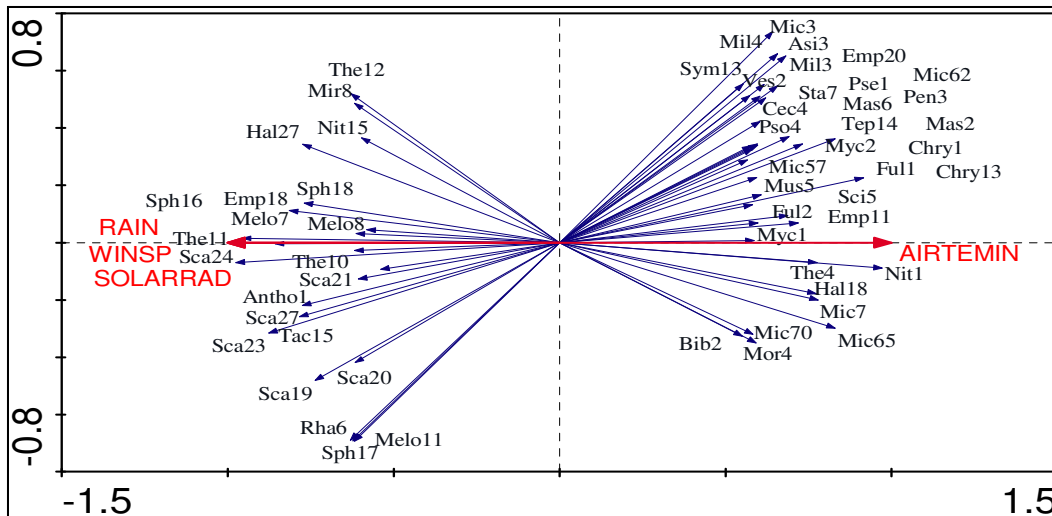
Figure 4.3D: Redundancy analysis (RDA) biplot of species and climatic variables for spring, using combined grid data. Only species that have their abundances explained by the first axis are shown (Appendix 1). Axis 1 and 2 respectively explain 25.8% and 18.2% variance in species-environmental relation. Monte-Carlo test of significance of all canonical axes: F = 2.439, p = 0.032. Climatic variable names: RAIN= Average rainfall, AIRTEMIN= Average minimum air temperature, WINSP= Average wind speed, SOLARRAD= Average solar radiation.

4.3.2 Land use effects.

Vegetation and climatic changes

In summer, plant species richness was 2.7 ± 1.4 (mean ± standard deviation) in cultivated sites while plant species richness in the heavily and lightly grazed sites were 5.3 ± 1.7 and 7.2 ± 1.6 respectively (F $_{(2, 24)}$ = 19.000, p = 0.0001) (Table 3.3). In autumn there were 2.1 ± 1.2, 4.9 ± 1.5 and 5.8 ± 1.0 plant species in cultivated, heavily and lightly

grazed sites respectively ($F_{(2, 24)}$ = 22.365, p = 0.0000). 8.1 ± 2.9, 9.2 ± 2.0 and 10.7 ± 1.9 plant species were recorded in cultivated, heavily and lightly grazed sites respectively in winter ($F_{(2, 24)}$ = 1.375, p = 0.272) while in spring, the plant species numbers were 4.8 ± 1.6, 9.2 ± 2.0 and 10.7 ± 1.9 for cultivated, heavily grazed and lightly grazed respectively ($F_{(2, 24)}$ = 24.481, p = 0.0000) (Table 3.3).

Table 3.4 chapter 3, shows mean percentage cover for annuals, rocks, grasses, bare ground, non succulent perennials and succulent perennials. Annuals had significantly higher cover in cultivated and heavily grazed sites than in lightly grazed sites. This trend was observed in winter (Z = 2.975, p = 0.003) and spring (Z = 3.417, p = 0.0006). Percentage cover of bare ground was highest in cultivated and lowest in lightly grazed sites through out all the seasons (summer, Z = 3.595, p = 0.003, autumn, Z = 2.932, p = 0.003, winter, Z = 3.146, p = 0.002 and spring, Z = 3.591, p = 0.003). The opposite was true for rock cover (summer, Z = 3.230, p = 0.001, autumn, Z = 3.241, p = 0.001, winter, Z = 2.419, p = 0.016 and spring, Z = 1.158, p = 0.247). Non-succulent perennials had significantly higher cover in cultivated compared to the grazed sites in summer (Z = 2.038, p = 0.042) and autumn (Z = 3.512, p = 0.0004). In winter the difference was only significant between cultivated and heavily grazed sites (Z = 2.083, p = 0.037) and in spring there were no significant differences (Z = 1.677, p = 0.093) (Table 3.4, chapter 3). The succulent perennials and succulent perennials with a height less of than 25 cm decreased significantly in the order lightly grazed, heavily grazed and cultivated for all seasons (Succulent perennials: summer, Z = 3.108, p = 0.004, autumn, Z = 3.700, p = 0.0002, winter, Z = 2.062, p = 0.039 and spring, Z = 2.708, p = 0.007, succulent perennials > 25 cm: summer, Z = 3.108, p = 0.002, autumn, Z = 2.762, p = 0.006, winter, Z = 2.809, p = 0.0005 and spring, Z = 3.547, p = 0.0004) (Tables 3.4 and 3.5, chapter 3). The opposite trend was observed for non-succulent perennials with a height of less than 25 cm, decreasing in the order: cultivated, heavily grazed and lightly grazed, though the difference between the cultivated and heavily grazed sites was only significant in autumn (Z = 3.382, p = 0.0007). Succulent perennials with a height greater than 25 cm were more dominant in lightly grazed sites, though only significantly different from heavily grazed in spring (Z = 3.138, p = 0.009) and autumn (Z = 3.112, p = 0.002).

G. africana had the high cover in cultivated sites for all seasons, as was the case for heavily grazed sites, except in spring when an annual sp.1 had the highest cover (Table 3.6). However, cover of *G. africana* was about two to three times more in cultivated than heavily grazed sites. *E. africanus* had the highest cover in lightly grazed sites in autumn, winter and spring while in summer *L. schultzei* was dominant.

Rainfall began peaking during the end of autumn (April to May) and reached a peak in winter (August) (Figure 3.6A, chapter 3). Air temperature and solar radiation were highest during summer sampling period, followed by autumn sampling period while these were minimal in winter (Figures 3.6B and 3.6C, chapter 3). The relative humidity of the air was lowest during autumn sampling (Figure 3.6D, chapter 3). Wind speed was constant during all sampling periods, (Figure 3.6E, chapter 3).

Insect species richness and abundance

The differences in assemblages for the land use types were unique for each season. Peaks in Hemiptera in summer were a result of high relative abundance (75.3%) in cultivated sites where there were eighteen species in all (APPENDICES 2A and 2B). Hymenoptera had the highest relative abundances on lightly grazed sites (47.6% and 46 species) (APPENDICES 2A and 2B). Cicadellidae (Hemiptera) were significantly more abundant in the cultivated sites (KW-H $_{(2, 9)}$ = 6.489, p = 0.039) (Table 4.2A) while Coleoptera: Buprestidae were the only Coleoptera pollinator family (Struck 1994a) which was species rich in cultivated sites (Z= 2.121, p = 0.033) (Table 4.2B). The pollinator family Hymenoptera: Fideliidae (Struck 1994a) was significantly more abundant in heavily grazed sites compared to cultivated sites (Z = 1.963, p = 0.049). Most pollinator families (Struck 1994a, b) were more abundant in lightly grazed sites compared to cultivated sites. These were Anthophoridae, Bombyliidae (Diptera), Halictidae, Megachilidae (Hymenoptera) and Melittidae, all with Z = 1.963, p = 0.049. Other taxa with high abundances in lightly grazed sites compared to cultivated sites were Lycaenidae

(Lepidoptera), the saprophytic scavengers Muscidae (Diptera) (Barraclough & Londt 1985) and parasitoids (Symphyta) (Prinsloo 1985) , all with Z =1.963, p = 0.049.

Peaks observed in Diptera in autumn were due to high relative abundances and species richness in lightly grazed (63.8% and 67 species) and cultivated sites (53 % and 77 species) (APPENDICES 2A and 2B). Hymenoptera followed in relative abundances in cultivated; 33.7% and 75 species (APPENDICES 2A and 2B). Conopidae was the most abundant Diptera family in cultivated sites (KW-H $_{2, 9}$ = 7.624, p = 0.022), as were the Mordellidae (Coleoptera) (KW-H $_{2, 9}$ = 6.720, p = 0.036 and Masaridae (Hymenoptera) (Z = 1.964, p = 0.049) (Table 4.2A). Pollinators (Struck 1994a) with significantly higher abundances in these sites were Melittidae (KW-H $_{2, 9}$ = 7.200, p = 0.027), Anthophoridae (Z = 1.993, p = 0.046) and Sphecidae (Z = 1.964, p = 0.049) (Tables 4.2A) while the families with significantly higher species richness compared to grazed sites were Conopidae (KW-H $_{2,9}$ = 8.000, p = 0.025), Halictidae (KW-H $_{2,9}$ = 6.214, p = 0.043) and Hymenoptera: Sphecidae (Z = 1.964, p = 0.049). Cicadellidae (KW-H $_{2, 9}$ = 6.489, p = 0.039) and Microlepidoptera (Z = 1.964, p = 0.049) were significantly more abundant in heavily grazed sites compared to lightly grazed and cultivated, as were Lepidoptera: Pieridae (Z = 1.964, p = 0.049) which were significantly higher in lightly grazed sites compared to the other land use types (Table 4.2A).

In winter, relative abundances of Coleoptera were 67.3%, 62.8% and 38.4% in heavily grazed, lightly grazed and cultivated sites, with 117, 17 and 14 species respectively (APPENDICES 2A and 2B). The Diptera families; Agromyzidae and Mycetophilidae were significantly more abundant in cultivated sites compared to grazed sites, Z = 1.964, p = 0.049, for both families. Microlepidoptera were both more abundant (Z = 1.964, p = 0.049) and species rich (Z = 1.993, p = 0.046) in cultivated sites. Mycetophilidae was however species rich in heavily grazed sites (KW-H $_{2, 9}$ = 6.438, p = 0.033). Diptera: Sciaridae and Coleoptera: Nitidulidae were more abundant in heavily grazed compared to cultivated sites (Z = 1.964, p = 0.049 for Nitidulidae and Z = 2.086, p = 0.036 for Sciaridae) (Table 4.2A). Muscidae were more abundant (Z = 1.964, p = 0.049) and species rich (Z= 2.121, p = 0.033) in lightly grazed sites compared to cultivated. Also in

lightly grazed sites, abundances for Coleoptera: Chrysomelidae (Z = 1.964, p = 0.049) and Diptera: Rhagionidae (Z = 1.993, p = 0.046) were higher compared to cultivated sites (Table 4.2A).

In spring, Diptera were the most abundant with 77.3% and 98 species in heavily grazed sites, followed by cultivated and lightly grazed sites with 44.2% and 41.5% relative abundance and 86 and 102 species respectively (APPENDICES 2A and 2B). Cicadellidae (Z = 1.964, p = 0.049) and Coleoptera: Meloidae (Z = 1.964, p = 0.049) and the pollinator families (Struck 1994a) Scarabaeidae: Hopliini (Z = 1.964, p = 0.049) and Sphecidae (Z = 1.964, p = 0.049) were significantly higher in abundance in cultivated sites, with Sphecidae (Z = 1.993, p = 0.046) having higher species richness in these sites (Tables 4.2A and 4.2B) compared to the heavily and lightly grazed sites. Sciaridae (KW-H $_{2,9}$ = 6.489, p = 0.039) were significantly abundant in heavily grazed sites compared to the other land uses, while the number of species was highest for Hemiptera: Lygaeidae (KW-H $_{2,9}$ = 6.150, p = 0.046) and Microlepidoptera (Z = 2.023, p = 0.043) in these sites. Symphyta were more abundant in lightly grazed sites compared to heavily grazed sites (Z = 1.993, p = 0.046) while Buprestidae were both abundant ((Z = 1.964, p = 0.049) and with higher species number (Z = 1.993, p = 0.046) in lightly grazed sites (Tables 4.2A and 4.2B).

Table 4.2A: Mean (± SD) relative abundance of flying insect taxa for the three land use types; cultivated, heavily grazed and lightly grazed, obtained using combined grid data. Taxa without the H-Value were not significant with Kruskal-Wallis but with Mann-Whitney tests. Degree of freedom=2, n= 9. * p<0.05, ** p<0.01, *** p<0.001. Species indicated with (#) are pollinators (Struck 1994a). Sig. means significance level.

	Cultivated	Heavily grazed	Lightly grazed	H-Value	p-value	Signif
SUMMER						
Hemiptera						
Alydidae	0.11 ± 0.040 a	---	0.14 ± 0.244 ab	---	0.037	*
Cicadellidae	69.82 ± 14.674 a	20.59 ± 15.718 b	4.75 ± 5.530 b	6.489	0.039	*
Coleoptera						
Coccinellidae	0.13 ± 0.010 a	---	0.32 ± 0.558 ab	---	0.037	*
Nitidulidae	0.29 ± 0.233 ab	0.51 ± 0.562 a	0.00 ± 0.000 b	---	0.049	*
Diptera						
Agromyzidae	0.34 ± 0.259 a	3.29 ± 2.235 b	3.12 ± 2.501 b	---	0.049	*
#Bombyliidae	0.68 ± 0.437 a	2.75 ± 1.253 b	4.20 ± 2.826 b	---	0.049	*
Muscidae	0.95 ± 1.033 a	7.32 ± 3.915 b	17.101 ± 7.510 b	---	0.049	*
Rhagionidae	0.48 ± 0.625 a	1.91 ± 1.425 ab	2.71 ± 0.183 b	---	0.037	*
Agromyzidae	0.34 ± 0.259 a	3.29 ± 2.235 b	3.12 ± 2.501 b	---	0.049	*
Sciaridae	0.21 ± 0.194 a	---	0.48 ± 0.837 ab	---	0.049	*
Fannidae	0.32 ± 0.193 a	---	0.16 ± 0.279 ab	---	0.037	*
Lepidoptera						
Lycaenidae	0.08 ± 0.073 a	0.19 ± 0.321 ab	0.84 ± 0.340 b	---		*
Hymenoptera						
#Halictidae	7.73 ± 4.445 a	25.96 ± 4.282 b	28.33 ± 12.866 b	---	0.049	*
#Megachilidae	0.18 ± 0.076 a	0.85 ± 0.383 a	0.98 ± 0.628 b	---	0.049	*
#Melittidae	3.10 ± 1.282 a	7.95 ± 5.216 ab	9.70 ± 6.327 b	---	0.049	*
Chalcididae	0.42 ± 0.210 a	0.78 ± 0.501 a	1.68 ± 0.566 b	---	0.049	*
#Anthophoridae	0.09 ± 0.079 a	0.71 ± 0.620 ab	1.66 ± 1.351 b	---	0.049	*
#Fideliidae	0.50 ± 0.448 a	1.70 ± 0.689 b	0.68 ± 0.38 ab	---	0.049	*
Symphyta	0.11 ± 0.138 a	0.14 ± 0.238 ab	0.89 ± 0.533 b	---	0.049	*
AUTUMN						
Hemiptera						
Cicadellidae	4.06 ± 1.459 a	11.18 ± 4.676 b	1.76 ± 1.299 a	6.489	0.039	*
Fulgoridae	0.40 ± 0.280 a	5.59 ± 4.715 b	2.84 ± 3.461 ab	---	0.049	*
Coleoptera						
Mordellidae	0.44 ± 0.146 a	---	0.07 ± 0.119 b	6.720	0.036	*

Nitidulidae	1.12 ± 0.517 a	0.14 ± 0.237 b	1.18 ± 0.152 b	---	0.046	*
Diptera						
Anthomyidae	0.28 ± 0.094 a	0.12 ± 0.213 ab	0.06 ± 0.068 b	---	0.049	*
Muscidae	0.93 ± 0.471 a	2.69 ± 1.253 b	4.83 ± 3.269 ab	---	0.049	*
Calliphoridae	0.46 ± 0.176 a	0.57 ± 0.203 a	0.03 ± 0.060 b	---	0.049	*
Phoridae	0.16 ± 0.106 a	2.91 ± 4.591 a	---	6.161	0.037	*
Conopidae	0.09 ± 0.002a	---	---	7.624	0.022	*
Empididae	0.77 ± 0.380 a	0.26 ± 0.117 b	1.17 ± 0.852 a	---	0.049	*
Scenopinidae	8.55 ± 1.346 a	0.09 ± 0.153 b	6.10 ± 8.396 a	---	0.046	*
Tachinidae	1.12 ± 0.210 a	1.56 ± 1.491 a	0.53 ± 0.012 b	---	0.049	*
Therevidae	13.57 ± 1.085 a	7.52 ± 5.243 b	24.11 ± 13.610 ab	---	0.049	*
Lepidoptera						
Microlepidoptera	3.84 ± 0.847 a	29.87 ± 11.130 b	11.34 ± 8.488 a	---	0.049	*
Pieridae	0.16 ± 0.142 a	0.13 ± 0.123 a	0.98 ± 1.020 b	---	0.490	*
Hymenoptera						
Agromyzidae	1.03 ± 0.651 a	2.90 ± 0.733 b	1.00 ± 0.874 a	---	0.049	*
#Anthophoridae	1.11 ± 1.224 a	0.05 ± 0.079 b	0.32 ± 0.443 ab	---	0.046	*
#Fideliidae	0.18 ± 0.316 ab	0.467 ± 0.342 a	---	---	0.037	*
#Melittidae	2.90 ± 0.597 a	0.09 ± 0.078 b	1.16 ± 0.763 c	7.200	0.027	*
Masaridae	6.41 ± 0.187 a	0.78 ± 0.333 b	1.27 ± 1.851 ab	---	0.049	*
#Sphecidae	1.74 ± 1.140 a	0.23 ± 0.208 b	0.34 ± 0.472 ab	---	0.049	*
WINTER						
Hemiptera						
Aphididae	0.68 ± 0.455 a	0.10 ± 0.090 b	0.24 ± 0.225 ab	---	0.049	*
Cicadellidae	6.90 ± 3.408 a	4.29 ± 1.920 ab	1.34 ± 1.652 b	---	0.049	*
Coleoptera						
Chrysomelidae	2.08 ± 2.207 a	9.20 ± 10.332 b	9.22 ± 3.370 b	---	0.049	*
Nitidulidae	32.76 ± 7.680 a	51.52 ± 7.821 a	46.50 ± 17.673 ab	---	0.049	*
Diptera						
Agromyzidae	9.43 ± 6.610 a	0.57 ± 0.73 b	0.28 ± 0.313 b	---	0.049	*
Empididae	3.50 ± 2.157 a	2.54 ± 2.640 ab	1.18 ± 0.725 b	---	0.049	*
Muscidae	0.18 ± 0.158 a	0.72 ± 0.233 b	3.73 ± 5.733 ab	---	0.049	*
Mycetophilidae	12.37 ± 10.538 a	3.49 ± 0.619 b	2.02 ± 0.197 b	---	0.049	*
Rhagionidae	0.12 ± 0.205 a	0.82 ± 1.228 ab	1.63 ± 1.140 b	---	0.046	*

Sciaridae	---	2.35 ± 1.275 b	1.51 ± 1.172 b	---	0.037	*
Lepidoptera						
Microlepidoptera	2.05 ± 0.863 a	0.31 ± 0.152 b	0.37 ± 0.217 b	---	0.049	*
SPRING						
Hemiptera						
Cicadellidae	6.41 ± 0.640 a	1.79 ± 1.269 ab	1.31 ± 0.496 b	---	0.049	*
Fulgoridae	---	0.43 ± 0.534 b	0.62 ± 0.653 ab	---	0.037	*
Pentatomidae	---	0.34 ± 0.450 b	0.43 ± 0.383 b	6.161	0.046	*
Coleoptera						
Chrysomelidae	0.19 ± 0.177 a	0.71 ± 0.580 ab	0.89 ± 0.424 b	---	0.049	*
Meloidae	9.72 ± 2.480 a	1.84 ± 1.564 b	1.88 ± 1.155 b	---	0.049	*
#Buprestidae	0.11 ± 0.191 ab	0.03 ± 0.055 a	0.56 ± 0.289 b	---	0.046	*
#Scarabaeidae	14.46 ± 3.765 a	2.78 ± 2.35 b	12.35 ± 7.931 ab	---	0.049	*
Staphylinidae	0.04 ± 0.067 b	0.04 ± 0.075 b	0.40 ± 0.196 a	---	0.046	*
Diptera						
Cecidomyiidae	0.11 ± 0.111 a	0.13 ± 0.226 ab	0.33 ± 0.040 b	---	0.049	*
Chloropidae	0.23 ± 0.233 a	0.27 ± 0.350 ab	0.82 ± 0.243 b	---	0.049	*
Asilidae	---	0.31 ± 0.137 b	0.58 ± 0.136 c	7.448	0.035	*
Fannidae	1.11 ± 1.629 a	0.14 ± 0.041 ab	0.04 ± 0.066 b	---	0.049	*
Milichiidae	0.26 ± 0.355 a	9.20 ± 5.984 b	10.48 ± 4.979 b	---	0.049	*
Mycetophilidae	---	1.68 ± 1.378 b	2.13 ± 3.094 b	---	0.037	*
Tachinidae	1.80 ± 0.227 a	0.34 ± 0.293 b	0.85 ± 0.697 ab	---	0.049	*
Therevidae	23.92 ± 10.547 a	9.21 ± 10.425 ab	6.12 ± 2.299 b	---	0.049	*
Rhagionidae	0.440.481 a	---	0.00 ± 0.000 b	7.624	0.022	*
Sciaridae	0.64 ± 0.282 a	33.27 ± 39.306 b	5.30 ± 5.157 b	6.489	0.039	*
Sepsidae	0.37 ± 0.276 a	---	0.04 ± 0.066 b	6.720	0.035	*
Lepidoptera						
Pieridae	0.150.131 ab	0.00 ± 0.000 a	0.21 ± 0.138 b	---	0.037	*
Hymenoptera						
Bethylidae	---	0.03 ± 0.055 a	0.19 ± 0.042 b	6.720	0.024	*
Masaridae	0.38 ± 0.060 a	1.07 ± 1.033 ab	1.74 ± 1.136 b	---	0.049	*
Scolebythidae	0.11 ± 0.192 a	---	2.72 ± 0.775 b	6.720	0.035	*
#Sphecidae	6.88 ± 1.162 a	2.76 ± 2.838 b	2.99 ± 1.413 b	---	0.049	*
Symphyta	0.38 ± 0.341 ab	0.19 ± 0.196 a	0.65 ± 0.091 b	---	0.049	
#Vespidae	---	0.17 ± 0.194 ab	0.20 ± 0.088 b	---	0.036	*

Table 4.2B: Mean (±SD) species richness of flying insect taxa for the three land use types; cultivated, heavily grazed and lightly grazed, obtained using combined grid data. Taxa without the H-Value were not significant with Kruskal-Wallis but with Mann-Whitney tests. Degree of freedom=2, n= 9. Sig. is significance level: * p<0.05, ** p<0.01, ***p<0.001. Species indicated with (#) are pollinators (Struck 1994 a).

	Cultivated	Heavily grazed	Lightly grazed	H-value	p-value	Signif.
SUMMER						
Hemiptera						
Alydidae	1.00 ± 0.000 a	---	0.03 ± 0.577 ab	---	0.025	*
Coleoptera						
#Buprestidae	2.33 ± 0.577 a	1.00 ± 0.000 b	0.67 ± 1.155 b	---	0.033	*
Coccinellidae	1.00 ± 0.000 a	---	0.33 ± 0.577 c	---	0.025	*
Diptera						
Fannidae	1.67 ± 1.155 a	---	0.33 ± 0.577 c	---	0.033	*
Sciaridae	1.00 ± 0.000 a	---	0.67 ± 1.155 c	---	0.025	*
AUTUMN						
Coleoptera						
Mordellidae	1.67 ± 0.577 a	---	0.67 ± 1.155 ab	---	0.033	*
Diptera						
Calliphoridae	3.33 ± 1.528 a	2.00 ± 1.000 ab	0.33 ± 0.577 b	---		*
Conopidae	1.00 ± 0.000 a	---	---	8.000	0.025	*
Phoridae	1.33 ± 0.577a	2.33 ± 0.577 a	---	7.015	0.033	*
Tachinidae	5.67 ± 0.577a	3.00 ± 1.000 b	2.00 ± 1.000 b	6.108	0.046	*
Hymenoptera						
#Fideliidae	0.33 ± 0.577a	1.00 ± 0.000 b	---	---	0.025	*
#Halictidae	11.33 ± 2.309 a	8.67 ± 0.577 b	6.67 ± 2.082 b	6.214	0.043	*
Masaridae	2.00 ± 0.000 a	3.67 ± 1.155 b	1.67 ± 1.155 ab	---	0.033	*
#Melittidae	6.33 ± 1.528 a	0.67 ± 0.577 b	4.00 ± 3.606 ab	---	0.046	*
#Sphecidae	4.00 ± 1.000 a	1.00 ± 1.000 b	1.67 ± 2.082 b	---	0.049	*
WINTER						
Diptera						
Chironomidae	1.00 ± 1.000 a	0.67 ± 1.155 ab	---	---	0.025	*
Muscidae	0.67 ± 0.577 a	2.00 ± 0.000 b	2.33 ± 1.528 ab	---	0.033	*
Mycetophilidae	1.00 ± 0.000 a	2.33 ± 0.577 b	3.33 ± 1.155 b	6.438	0.033	*
Sciaridae	---	1.00 ± 0.000 b	1.00 ± 0.000 b	8.000	0.033	*

Lepidoptera

Microlepidoptera	4.00 ± 1.000 a	1.67 ± 0.577 b	2.00 ± 1.732 ab	---	0.046	*

SPRING

Hemiptera

Pentatomidae	---	1.00 ± 0.000 b	1.67 ± 0.577 b	7.086	0.029	*
Fulgoridae	---	1.33 ± 0.577 b	1.00 ± 1.000 ab	---	0.034	*
Lygaeidae	2.33 ± 1.155 ab	3.67 ± 0.577 a	0.67 ± 0.577 b	6.150	0.046	*

Coleoptera

#Buprestidae	0.33 ± 0.577 a	0.33 ± 0.577 a	3.00 ± 1.000 b	---	0.046	*
Nitidulidae	4.33 ± 2.517 a	7.67 ± 0.577ab	8.67 ± 0.577 b	6.386	0.041	*

Diptera

Asilidae	---	1.67 ± 0.577 b	2.33 ± 0.577 b	6.742	0.034	*
Mycetophilidae	---	1.33 ± 0.577 b	1.33 ± 0.577 b	6.171	0.046	*
Rhagionidae	1.00 ± 0.000 a	---	---	8.000	0.018	*
Sepsidae	1.00 ± 0.000 a	---	0.33 ± 0.577 ab	---	0.025	*

Lepidoptera

Noctuidae	1.33 ± 1.528 a	2.00 ± 0.000 ab	3.67 ± 1.155 b	---	0.046	*
Pieridae	0.67 ± 0.577 ab	---	1.00 ± 0.000 b	---	0.025	*
Microlepidoptera	4.67 ± 2.887 a	12.00 ± 5.196 b	10.33 ± 3.786 ab	---	0.043	*

Hymenoptera

#Sphecidae	7.00 ± 2.000 a	6.33 ± 2.309 a	2.67 ± 0.577 b	---	0.043	*
#Vespidae	---	1.00 ± 0.000 b	1.00 ± 0.000 b	---	0.025	*
Bethylidae	---	0.33 ± 0.577 ab	1.00 ± 0.000 b	---	0.025	*
Masaridae	1.33 ± 0.577 a	4.00 ± 2.000 ab	5.00 ± 2.000 b	---	0.046	*
#Milichiidae	0.67 ± 0.577 a	2.33 ± 0.577 b	2.00 ± 0.000 ab	6.788	0.034	*
Scolebythidae	0.33 ± 0.577 ab	---	1.00 ± 0.000 b	---	0..025	*

Species assemblages

RDA results for summer (Figure 4.4A) show the first axis represents habitat gradient of increasing non-succulent perennials, annuals and bare area which were negatively correlated with rock cover and succulent plant cover. Some Halictidae (abbreviated as: Hal1, Hal19 and Hal23) and Sphecidae (Sph3) increase in abundances with increasing cover of non-succulent perennials and bare area that dominate in cultivated areas. One Anthophoridae (Anth6) and Bombyliidae (Bom23) species were associated with lightly

grazed sites. Though the influence of all the environmental variables was not significant (p = 0.0620), the first axis accounted for 26.9% variance explained by species data and variance explained by the following axes decreased compared to the variance of the first axis (Figure 4.4A).

In autumn, the RDA triplots show the pollinator species (Struck 1994a) in cultivated (Hal17, Meg4 and Sph3) and heavily grazed (Hal15 and Mas14) sites increased in abundances with increasing bare ground and perennial plant cover. Most Halictidae species (Hal13, Hal14 and Hal18) were characteristic of lightly grazed sites, where succulent plant cover was high (Figure 4.4B). Though the influence of all the variables together was not significant, p = 0.052, the first two axes explained 41.4% of the variance in species data (Figure 4.4B).

The influence of the environmental variables was significant in winter season (F = 1.669, P = 0.010). The first two axes accounted for 46.4% variance explained by species data (Figure 4.4C). Perennial and annual plant cover in the cultivated sites had a major influence on assemblages in these sites. Succulents influenced assemblages in two of the lightly grazed sites, where abundance of three Halictidae (Hal14, Hal16 and Hal20) species were seen to increase (Figure 4.4C)

Percentage cover of perennials and bare ground were characteristic of cultivated sites. The Scarabaeidae: Hopliini (Sca20, Sca23, Sca24, Sca25 and Sca27) and Sphecidae (Sph15, Sph16 and Sph17) which had high abundances in spring tend to prefer high cover of annuals, bare ground and perennials (Figure 4.4D). The two axes of the RDA biplot account for 43.5% variance explained by species data (Figure 4.4D).
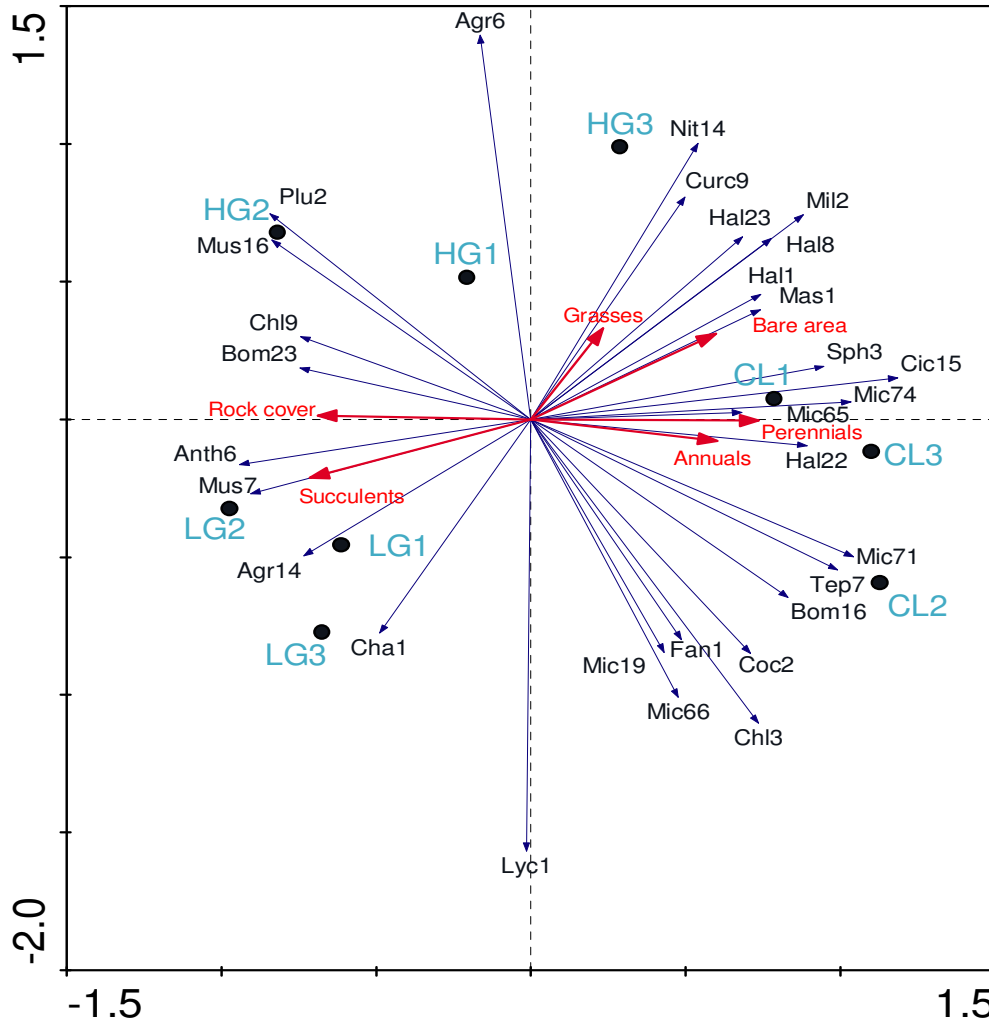
Figure 4.4A: Redundancy analysis (RDA) triplot of flying insect taxa and habitat variables (Sites for illustrative purposes) for summer, obtained using combined grid data. Only species (Appendix 1) that account for more than 26% of the variance explained are shown. Axes 1 and 2 respectively explain 26.9% and 14.6% of the species data. Monte-Carlo test for all canonical axes not significant, F = 1.361, p = 0.062. Site names: CL = cultivated, HG = heavily grazed, LG = lightly grazed. Numbers are the respective plot numbers for the different land uses. Succulents= succulent perennials and perennials= non succulent perennials.
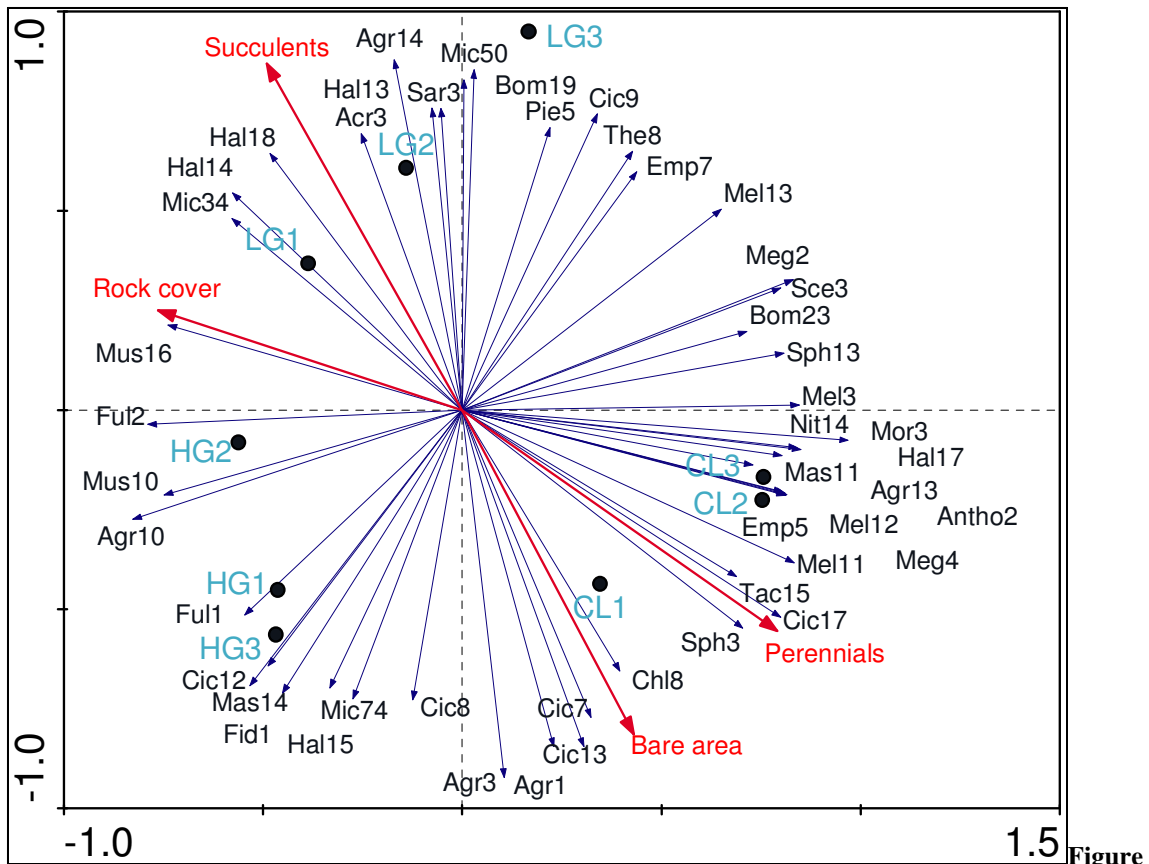
Figure 4.4B: Redundancy analysis (RDA) triplot of flying insect taxa and habitat variables (Sites for illustrative purposes) for autumn, obtained using combined grid data. Only species (Appendix 1) that account for more than 41% of the variance explained are shown. Axes 1 and 2 respectively explain 23.2% and 18.2% of the species data. Monte-Carlo test for all canonical axes not significant, F = 1.357, p = 0.052. Site names: CL = cultivated, HG = heavily grazed, LG = lightly grazed. Numbers are the respective plot numbers for the different land uses. Succulents= succulent perennials and perennials= non succulent perennials.
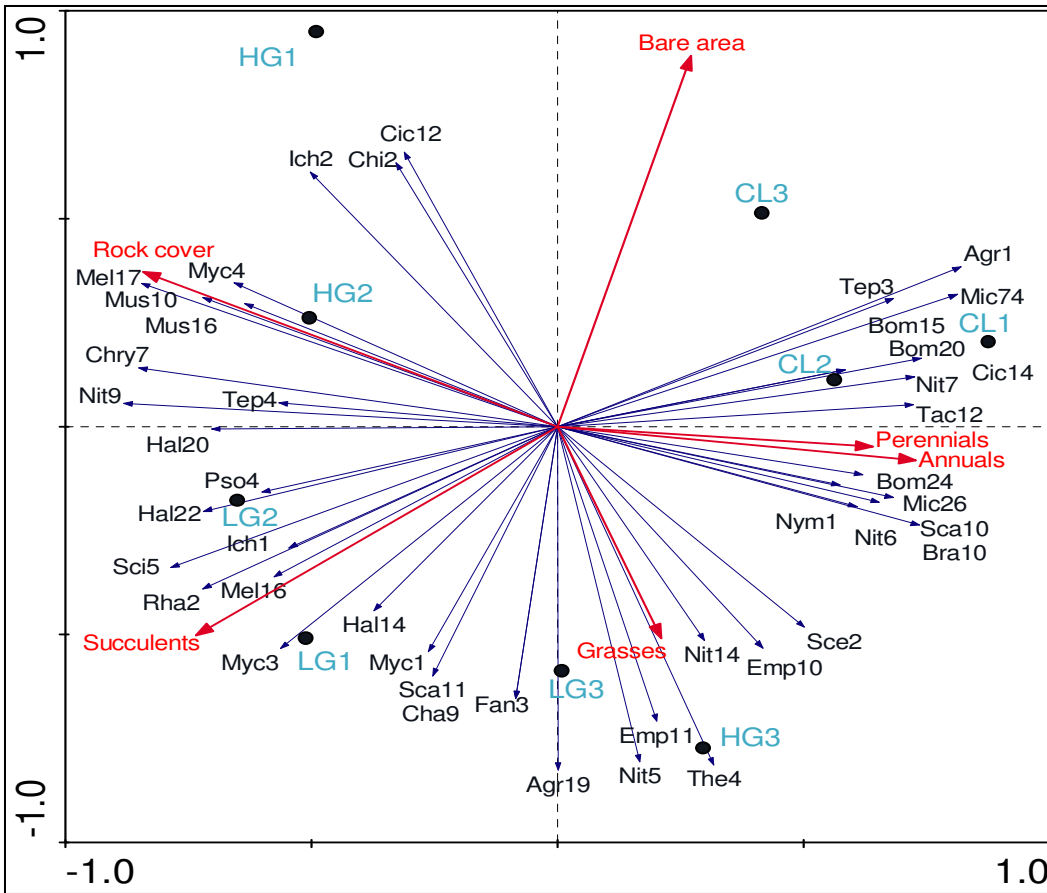
Figure 4.4C: Redundancy analysis (RDA) triplot of flying insect taxa and habitat variables (Sites for illustrative purposes) for winter, obtained using combined grid data. Only species (Appendix 1) that account for more than 32% of the variance explained are shown. Axes 1 and 2 respectively explain 32.3% and 14.1% of the species data. Monte-Carlo test for all canonical axes significant, $F = 1.669$, $p = 0.010$. Site names: CL = cultivated, HG = heavily grazed, LG = lightly grazed. Numbers are the respective plot numbers for the different land uses. Succulents= succulent perennials and perennials= non succulent perennials.
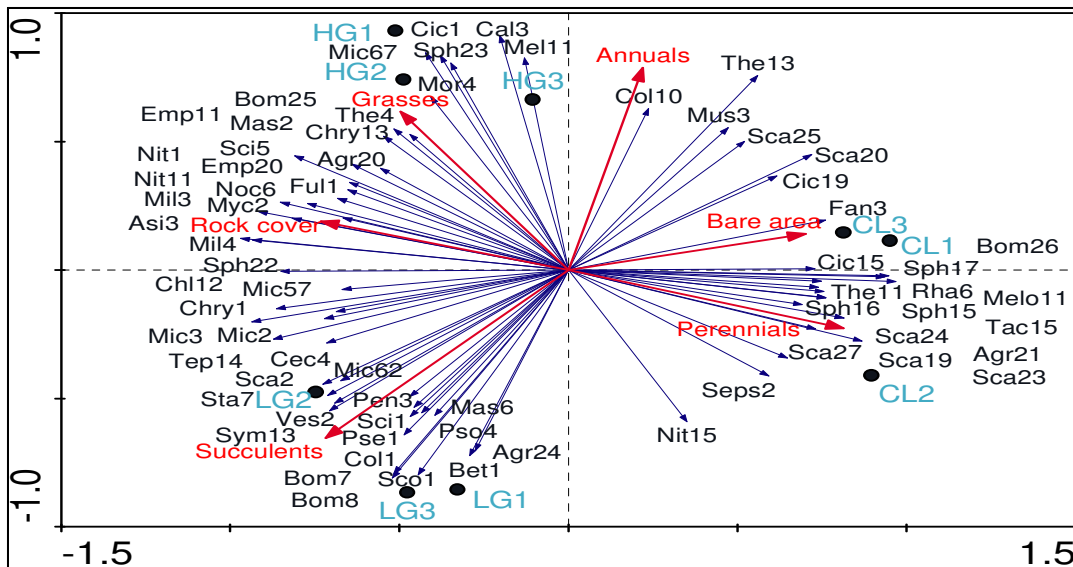
Figure 4.4D: Redundancy analysis (RDA) triplot of species flying insect taxa and habitat variables (Sites for illustrative purposes) for spring, obtained using combined grid data. Only species (Appendix 1) that account for more than 43% of the variance explained are shown. Axes 1 and 2 respectively explain 29.3% and 14.2% of the species data. Monte-Carlo test for all canonical axes not significant, F = 1.388, p = 0.092. Site names: CL = cultivated, HG = heavily grazed, LG = lightly grazed. Numbers are the respective plot numbers for the different land uses. Succulents= succulent perennials and perennials= non succulent perennials.

4.3.3 Indicator species

Almost all species that contributed to dissimilarity between land use types were found to be indicators for land use (Tables 4.3A, 4.3B, 4.3C and 4.3D). Based on the Indicator Value Method (INDVAL), indicators were specific for each season, with the few exceptions, such as Agromyzidae sp. 14, which was an indicator for the lightly grazed sites for both summer and autumn. Certain species were identified as indicators for different land use types for different seasons. Examples are Microlepidoptera sp. 74, Cicadellidae sp. 15, Mycetophilidae sp. 2 and Melittidae sp. 11 (Tables 4.3A, 4.3B, 4.3C and 4.3D). Summer and winter had the least number of indicator species, with the heavily grazed sites having no indicator species for winter (Tables 4.3A and 4.3B). In autumn, the two taxa Microlepidoptera and Halictidae contributed mostly to indicator species followed by Melittidae and Cicadellidae (Table 4.3C). In spring, Scarabaeidae and Sphecidae were the main contributors, followed by Microlepidoptera and Bombyliidae (Table 4.3D).

Figures 4.5A, 4.5B, 4.5C and 4.5D show results of cluster analyses for summer, autumn, winter and spring respectively. For all the seasons, samples formed two main clusters. The first group is composed of samples from Kleinfontein, with the cultivated sites forming distinct groups for every season. The other group is composed mostly of samples from Kuile, though these are not clearly discernible in terms of land use; except for autumn where the heavily grazed sites formed their own distinct group at 50% similarity level (Figure 4.5B). Winter was the only season where samples from Kleinfontein and Kuile formed two exclusive groups, though the Kleinfontein lightly grazed and heavily grazed sites were very similar. Stress values obtained with MDS ordination are 0.03, 0.08, 0.05 and 0.04 for summer, autumn, winter and spring respectively. These values are small enough to conclude that the produced ordinations reflect true rather than misleading results (Clarke & Warwick 2001).

ANOSIM results indicate that the differences obtained from cluster analysis based on land uses are statistically significant. Based on assemblage composition, differences between land use types were significant in summer, (R = 0.646, p = 0.014), in autumn, (R = 0.687, p = 0.004) and in spring (R = 0.770, p =0.007). ANOSIM did not reveal any significant land use differences in winter (R = 0.407, p = 0.068). However, ANOSIM test show pair-wise differences between land uses to be highest for cultivated and lightly grazed sites. R = 0.889 for summer, R = 0.963 for winter and R = 1.000 for spring between these two land use types. Autumn was the only season in which site differences were greatest between cultivated and heavily grazed sites; R = 0.963. For all the seasons, heavily grazed and lightly grazed sites had the least assemblage differences. SIMPER results also showed the average dissimilarity between cultivated and lightly grazed sites to be the highest for all the seasons (Tables 4.4A, 4.4B, 4. 4C and 4.4D).

Tables 4.4A, 4.4B, 4.4C and 4.4D also show the five species that contributed most to the dissimilarity between cultivated, heavily grazed and lightly grazed sites for all the four seasons. Species are arranged in order of decreasing contribution to total dissimilarity. Species that contributed to the dissimilarity between land uses differ between seasons, with the exception of Microlepidoptera sp. 74 which contributed to dissimilarity both in

summer and autumn and Sciaridae sp. 5 which contributed the dissimilarity in winter and spring.

Table 4.3: Percentage indicator values (INDVAL > 70%) of flying invertebrate species for **A)** Summer, **B)** winter , **C)** autumn and **D)** spring for each land use, obtained using combined grid data. Species proceeded by a star (*) are pollinators (Struck 1994 a).

A

Order	Species	% INDVAL		
		CL	HG	LG
Hemiptera	Cicadellidae sp.15	89.6		
Diptera	Tephritidae sp.7	77.8		
Diptera	*Bombyliidae sp.16	75.0		
Lepidoptera	Microlepidoptera sp.74	74.4		
Diptera	Chloropidae sp.3	71.4		
Diptera	Agromyzidae sp.6		74.2	
Diptera	Agromyzidae sp.14			80.0

B

Order	Species	% INDVAL		
		CL	HG	LG
Diptera	Agromyzidae sp. 141	100.0		
Lepidoptera	Microlepidoptera sp. 96	100.0		
Diptera	Mycetophilidae sp. 643	87.0		
Diptera	Mycetophilidae sp. 680			100.0
Diptera	Rhagionidae sp. 354			72.0

C

Order	Species	% INDVAL		
		CL	HG	LG
Hemiptera	Cicadellidae sp.17	95.7		
Hymenoptera	*Halictidae sp. 19	74.4		
Hymenoptera	*Halictidae sp. 17	72.2		
Hymenoptera	Masaridae sp.11	70.8		
Hymenoptera	*Melittidae sp. 3	80.0		
Hymenoptera	*Melittidae sp. 11	100.0		
Coleoptera	Mordellidae sp. 3	92.3		
Coleoptera	Nitidulidae sp. 14	90.6		
Hymenoptera	*Sphecidae sp.3	95.8		
Diptera	Tachinidae sp. 15	81.3		
Diptera	Agromyzidae sp. 10		87.5	
Hemiptera	Cicadellidae sp. 12		72.7	
Hemiptera	Cicadellidae sp. 15		77.2	
Hemiptera	Fulgoridae sp. 1		70.1	
Hymenoptera	*Halictidae sp. 8		82.8	
Hymenoptera	*Halictidae sp. 15		96.6	
Hymenoptera	Masaridae sp. 14		80.0	
Lepidoptera	Microlepidoptera sp. 28		90.0	
Lepidoptera	Microlepidoptera sp. 74		71.7	
Diptera	Muscidae sp. 10		80.0	
Diptera	Agromyzidae sp. 14			100.0
Hymenoptera	*Halictidae sp. 18			79.3
Lepidoptera	Microlepidoptera sp. 72			80.0
Lepidoptera	Microlepidoptera sp. 77			76.9
Lepidoptera	Pieridae sp. 5			83.3

D

Order	Species	% INDVAL		
		CL	HG	LG
Hemiptera	Cicadellidae sp. 15	75.7		
Diptera	Fannidae sp. 3	88.9		
Coleoptera	Meloidae sp. 11	100.0		
Diptera	Rhagionidae sp. 6	100.0		
Coleoptera	*Scarabaeidae sp. 19	97.2		
Coleoptera	*Scarabaeidae sp. 23	75.8		
Hymenoptera	*Sphecidae sp. 16	72.3		
Hymenoptera	*Sphecidae sp. 17	100.0		
Diptera	Tachinidae sp. 15	81.3		
Diptera	Calliphoridae sp. 3		80.0	
Hemiptera	Cicadellidae sp. 1		100.0	
Diptera	Empididae sp. 20		71.4	
Hymenoptera	Masaridae sp. 2		70.6	
Hymenoptera	*Melittidae sp. 11		91.7	
Lepidoptera	Microlepidoptera sp. 67		100.0	
Lepidoptera	Microlepidoptera sp. 68		75.8	
Diptera	Mycetophilidae sp. 2		73.8	
Diptera	Sciaridae sp. 5		94.5	
Hymenoptera	*Sphecidae sp. 23		100.0	
Hemiptera	Agromyzidae sp. 24			85.7
Diptera	*Bombyliidae sp. 7			100.0
Diptera	*Bombyliidae sp. 8			100.0
Coleoptera	*Buprestidae sp. 9			71.4
Lepidoptera	Microlepidoptera sp. 62			90.0
Coleoptera	*Scarabaeidae sp. 2			80.0
Hymenoptera	Scolebythidae sp. 1			98.2
Coleoptera	Staphylinidae sp. 7			85.7
Diptera	Tephritidae sp. 14			71.4
Hymenoptera	Vespidae sp.2			80.0
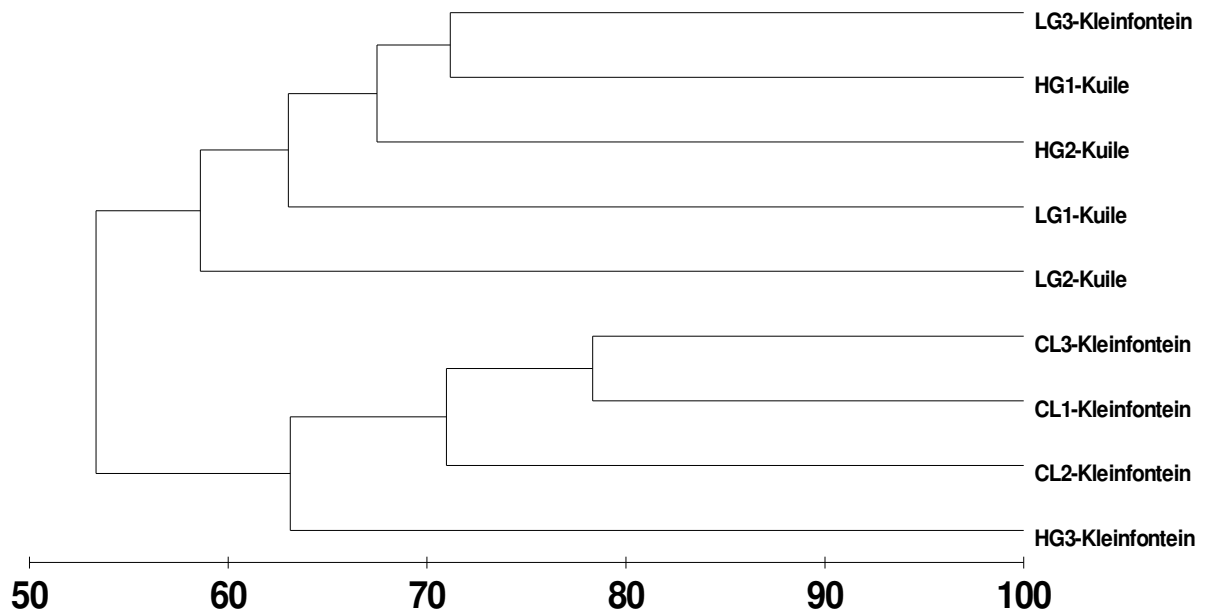
Figure 4.5A: Dendogram based on Bray-Curtis similarity matrix for the square root transformed data for summer, obtained using combined grid data. Site names: CL = Cultivated, HG = heavily grazed, LG = lightly grazed. Kleinfontein and Kuile are the two locations where sampling was conducted.
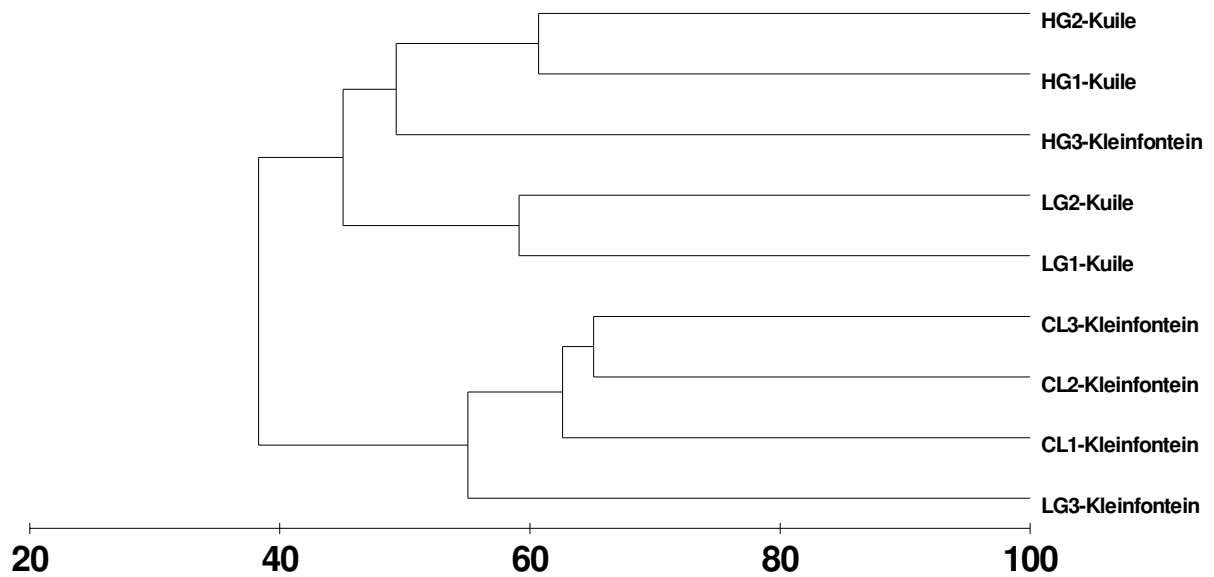
Figure 4.5B: Dendogram based on Bray-Curtis similarity matrix for the square root transformed data for autumn, obtained using combined grid data. Site names: CL = Cultivated, HG = heavily grazed, LG = lightly grazed. Kleinfontein and Kuile are the two locations where sampling was conducted.

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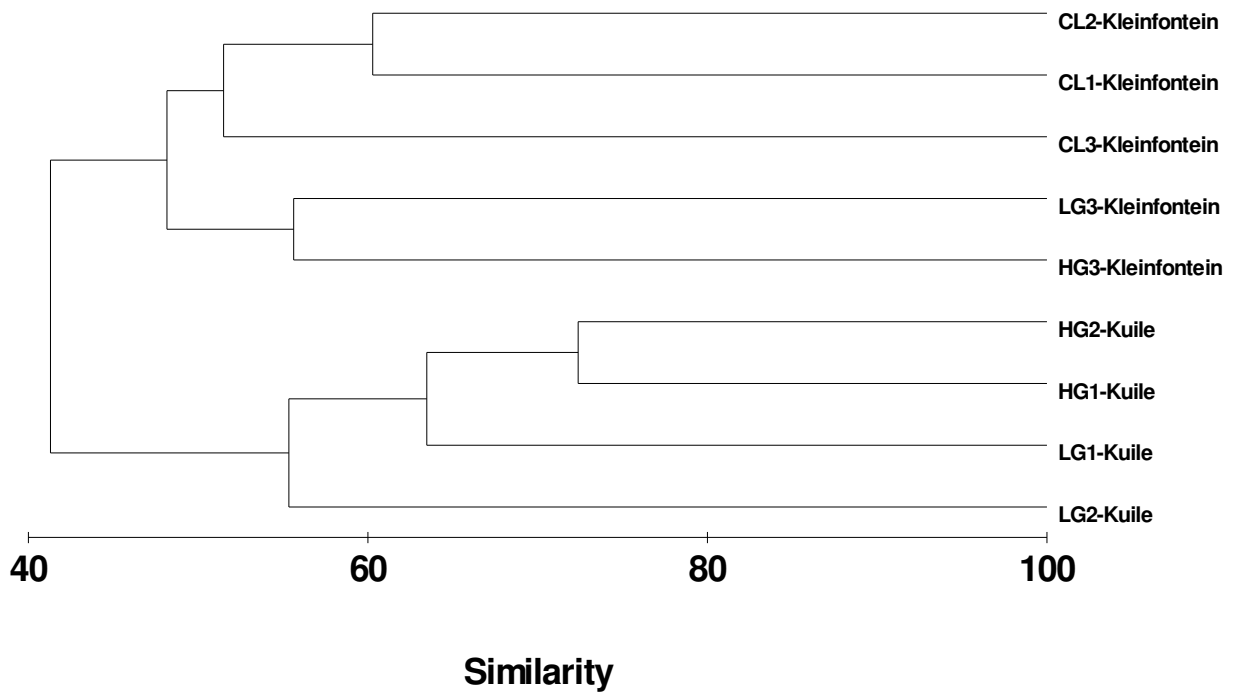
Figure 4.5C: Dendogram based on Bray-Curtis similarity matrix for the square root transformed data for winter, obtained using combined grid data. Site names: CL = Cultivated, HG = heavily grazed, LG = lightly grazed. Kleinfontein and Kuile are the two locations where sampling was conducted.
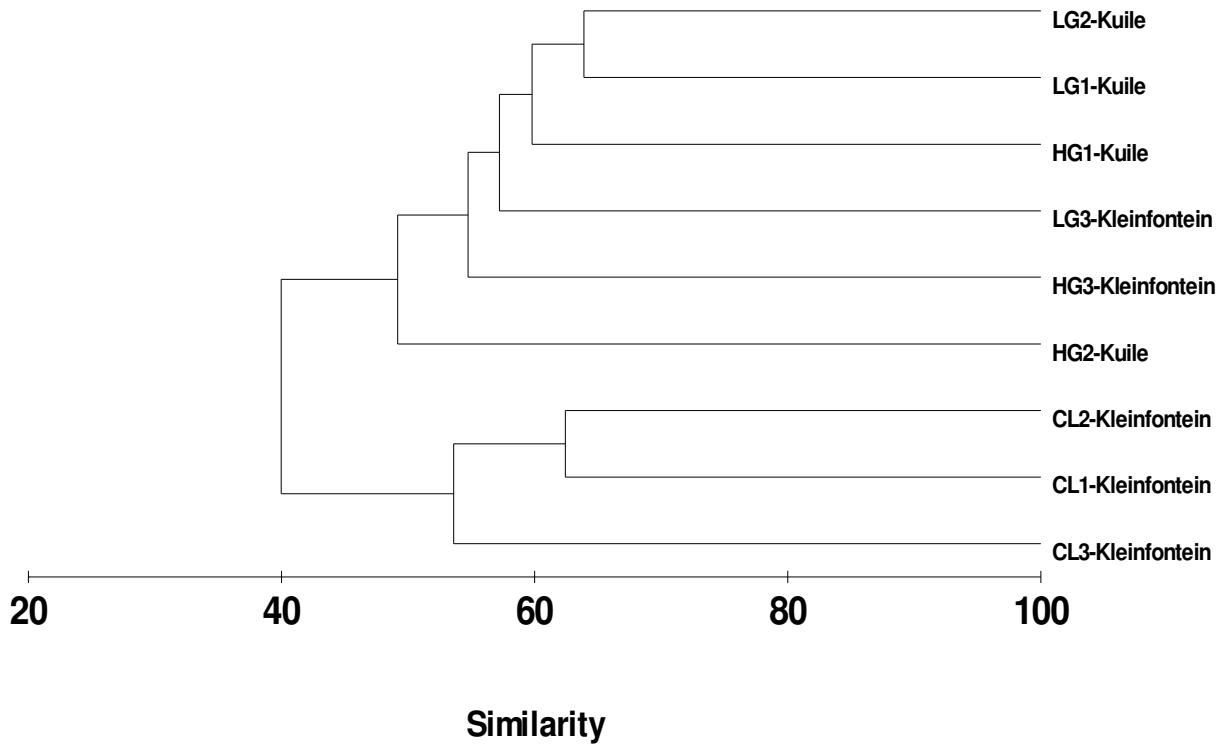
Figure 4.5D: Dendogram based on Bray-Curtis similarity matrix for the square root transformed data for spring, obtained using combined grid data. Site names: CL = Cultivated, HG = heavily grazed, LG = lightly grazed. Kleinfontein and Kuile are the two locations where sampling was conducted.

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Table 4.4A: Average dissimilarity between flying insect assemblages from the different land use types for **summer,** obtained using combined grid data. Taxa are arranged in order of decreasing contribution and only top five contributors shown Species indicated with (*) are pollinators (Struck 1994a, b).

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
Cultivated and heavily grazed (Average dissimilarity = 34.40)	Cicadellidae sp.15	6.95	6.95
	Chloropidae sp.3	4.34	11.29
	Microlepidoptera sp.71	3.37	14.66
	Coccinellidae sp.2	3.10	17.76
	*Bombyliidae sp.16	2.94	20.71
Cultivated and lightly grazed (Average dissimilarity = 40.49)	Cicadellidae sp.15	9.07	9.07
	Microlepidoptera sp.74	3.65	12.72
	Agromyzidae sp.14	3.57	16.29
	Masaridae sp.1	2.89	19.18
	Milichiidae sp.2	2.80	21.98
Heavily and lightly grazed (Average dissimilarity = 35.50)	Cicadellidae sp.15	3.69	3.69
	Agromyzidae sp.6	3.60	7.29
	Lycaenidae sp.1	3.47	10.76
	Agromyzidae sp.14	3.33	14.09
	*Apidae sp.2	2.94	17.03

Table 4.4B: Average dissimilarity between flying insect assemblages from the different land use types for **autumn** obtained using combined grid data. Taxa are arranged in order of decreasing contribution and only top five contributors shown. Species indicated with (*) are pollinators (Struck 1994a, b).

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
Cultivated and heavily grazed (Average dissimilarity = 51.85)	Scenopinidae sp.3	2.55	2.55
	Microlepidoptera sp.28	1.69	4.24
	Microlepidoptera sp. 32	1.6	5.84
	Microlepidoptera sp. 34	1.55	7.39
	*Bombyliidae sp.23	1.47	8.86
Cultivated and lightly grazed (Average dissimilarity = 55.14)	Microlepidoptera sp.77	1.72	1.72
	Microlepidoptera sp. 34	1.49	3.21
	*Sphecidae sp. 3	1.44	4.65
	Cicadellidae sp. 17	1.43	6.08
	Masaridae sp. 11	1.41	7.49
Heavily and lightly grazed (Average dissimilarity = 54.50	*Halictidae sp. 15	2.14	2.14
	Scenopinidae sp. 3	2.03	4.17
	Microlepidoptera sp. 74	1.79	5.96
	Cicadellidae sp. 12	1.65	7.61
	*Halictidae sp. 8	1.62	9.23

Table 4.4C: Average dissimilarity between flying insect assemblages from the different land use types for **winter**, obtained using combined grid data. Taxa are arranged in order of decreasing contribution and only top five contributors shown. . Species indicated with (*) are pollinators (Struck 1994a, b).

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
Cultivated and heavily grazed (Average dissimilarity = 54.23)	Agromyzidae sp. 1	4.21	4.21
	Nitidulidae sp. 9	3.56	7.77
	Sciaridae sp. 51	3.47	11.24
	Mycetophilidae sp. 4	2.71	13.95
	Nitidulidae sp. 7	2.59	16.54
Cultivated and lightly grazed (Average dissimilarity = 55.59)	Agromyzidae sp. 1	4.04	4.04
	Rhagionidae sp. 2	2.98	7.02
	Nitidulidae sp. 9	2.9	9.92
	Sciaridae sp. 5	2.86	12.78
	Nitidulidae sp.7	2.75	15.53
Heavily and lightly grazed (Average dissimilarity = 42.84)	Therevidae sp.3	2.99	2.99
	Rhagionidae sp. 2	2.77	5.76
	Mycetophilidae sp. 3	2.69	8.45
	Nitidulidae sp. 12	2.67	11.12
	Mycetophilidae sp. 4	2.64	13.76

Table 4.4D: Average dissimilarity between flying insect invertebrate assemblages from the different land use types for **spring**, obtained using combined grid data. Taxa are arranged in order of decreasing contribution and only top five contributors shown. Species indicated with (*) are pollinators (Struck 1994a, b).

Land uses	Taxa	Dissimilarity %	Cumulative dissimilarity %
Cultivated and heavily grazed (Average dissimilarity = 52.40)	Sciaridae sp. 5	2.46	2.46
	Milichiidae sp. 14	2.27	4.73
	Mycetophilidae sp. 2	1.72	6.45
	*Sphecidae sp. 17	1.61	8.06
	Milichiidae sp. 3	1.51	9.57
Cultivated and lightly grazed (Average dissimilarity = 54.55)	Milichiidae sp. 14	2.02	2.02
	*Sphecidae sp. 17	1.59	3.61
	Coleoptera sp. 1	1.40	5.01
	Scolebythidae sp. 1	1.38	6.39
	Therevidae sp. 11	1.29	7.68
Heavily and lightly grazed (Average dissimilarity = 41.54)	Cicadellidae sp.15	2.04	2.04
	Agromyzidae sp.6	1.92	3.96
	Lycaenidae sp.1	1.44	5.40
	Agromyzidae sp.14	1.37	6.77
	*Apidae sp.2	1.32	8.09

4.4 Discussion

4.4.1 Seasonal differences

Invertebrates form the basis of ecosystem functions, are very sensitive to disturbance (Samways 1994) and because of their high abundance, their use as indicators of land use has recently been realized, especially in biodiversity in hotspots such as the Succulent Karoo (Myers *et al*. 2000; Colville *et al*. 2002)..However, to determine assemblage patterns, sampling techniques should be well conducted. In this study, it was impossible to have more replicates of land use and seasonal treatments due to time constraints. Resultantly, limited inferences about assemblage patterns could be made. The study would have benefited from more replications of land use types and more seasonal samplings. Factors affecting both temporal and spatial diversity of invertebrates, such as reproductive patterns, hibernation, climatic differences between sites and topographic

differences could result in different patterns emerging (Wolda 1988; Fabricius *et al.* 2003), and these could only be well established with increased replication.

The possible error in using coloured pan traps to compare flying invertebrate assemblages is that traps possibly compete with the surrounding vegetation in attracting the invertebrates. Mayer (2005) found no differences between the heavily grazed and moderately grazed sites in terms of the abundances and diversity of pollinator fauna when sampling with coloured pan traps, but with the use of malaise traps and transect counts, there were significant differences in diversity, richness and abundances between land uses. However, the fact that comparisons could be obtained at both order and family levels suggests that coloured pan traps provided a rigorous test of the assemblages in the present study. Also, differences were picked up during the flowering season, suggesting that despite the high floral displays, invertebrates were still attracted to and could still be caught with coloured traps. Coloured pan traps have been used in the Succulent Karoo in a number of studies, including Colville *et al.* (2002) and Picker & Midgley (1996), which were looking into assemblages of flying taxa. In both these studies, assemblages of Scarabaeidae: Hopliini at species level were determined and colour preferences also determined. The use of RTUs was appropriate because the aim of the study was to determine assemblage patterns, and not to determine species which constitute assemblages, also, only about five percent of invertebrates are known (Samways 1994). The disadvantage of using morphospecies was that with increasing seasonal sampling, more RTU's were encountered and this might have increased the possibility of errors due to clumping and splitting (Oliver & Beattie 1996).

In this study, changes across seasons were observed for overall species richness and diversity, while evenness and total abundance of invertebrates collected did not change. Species richness and diversity were significantly higher in spring compared to the other three seasons. Richness in autumn was also significantly higher than in winter and summer.

The high species richness of invertebrates in the Succulent Karoo (Vernon 1999) is attributable to the vast array of flowering plants in the area. Flowering occurred in late winter to spring, providing a vast array of resources for invertebrates including among others food, shelter, oviposition sites and mating sites (Kevan & Baker 1999; Kevan & Baker 1983; Atkins 1980; Edwards & Wratten 1980), resulting in increased flying insect richness and diversity. Evenness did not change significantly, as well as the overall abundances, though these were also higher in spring, also suggesting that increased resource availability could be a factor that lead to their slight increase.

The overall seasonal differences were also evident for both species richness and relative abundance of the different invertebrate orders. Coleoptera were significantly more abundant in winter in comparison to the other seasons. Hymenoptera and Lepidoptera were more abundant and species rich in summer and autumn. Diptera were significantly richer in spring than in any other season. The present study shows clear seasonal differences for the different invertebrate orders. This information forms the basis for other studies to follow in the Succulent Karoo and it means that depending on the objectives of the studies, these seasonal differences should be considered. In cases where there are time constraints, seasons with the highest abundance and/or richness for each target order should be considered for sampling. These results are similar to what Mayer (2004) found for Hymenoptera, Diptera, Lepidoptera and Coleoptera. These were the major contributors to the assemblage in spring sampling season while Seymour & Dean (1999) found the flying invertebrate assemblages to be largely made up of Coleoptera, Diptera, Hemiptera and Hymenoptera, though pitfalls were used and not coloured pan traps.

Mayer (2004) caught more Hymenoptera individuals in lightly grazed sites than heavily grazed, similar to spring results in this study. Mayer (2004) also determined that there were no differences in abundance and species numbers of Apoidea (bees) between heavily grazed and lightly grazed sites. In this study, Fideliidae was the only bee family with higher abundances in heavily grazed sites than any other land use type, though this

was only observed during the hotter summer and autumn seasons. These bees are known to be specialists, feeding on pollen and nectar of flowers of Mesembryanthemaceae (Whitehead 1984; Vernon 1999), with the hotter season species being more common in winter rainfall area (Whitehead 1984).

Seasonal differences in abundances and richness of invertebrates are not uncommon (Neff *et al*. 2007; Vohland *et al*. 2005). Invertebrates have evolved the ability to perceive environmental cues such as temperature, humidity and photoperiod (Goodwin & Danthanarayana 1984; Nechols *et al*. 1999) and undergo changes like diapause (Watanabe & Tanaka 1998; Wolda 1988), the timing of which is highly synchronised with seasonal changes (Davis *et al*. 2000). Average rainfall, wind speed, solar radiation and minimum temperature of the air were the climatic variables to which assemblages responded to in this study. The high abundance and richness of Lepidoptera in summer and autumn could have been a result of the high temperatures and solar radiation during these seasons. For Lepidoptera, the egg, larval and pupal stages decrease with increasing temperatures and survival rates and activity increase with temperature (Goodwin & Danthanarayana 1984). Field studies in Chrysomelidae (Coleoptera) show that the insects remain dormant until spring when post-diapause development occurs as a result of increasing temperatures (Watanabe & Tanaka 1998).

During low temperatures, most insects hibernate as, for instance, eggs as in the case of Aphididae (Strathdee *et al*. 1995) or as adults as in some Chrysomelidae (Davis *et al*. 2000). Low abundances and species richness in winter could have been the result of diapause in many of the species. Cold conditions also lower the foraging activity and flight patterns in insects (Picker & Midgley 1994; Struck 1994a) with the resultant low abundances in assemblages (Struck 1994a, b). However, Wolda (1988) warns that the general impression that insects cannot be active during the cold season is not always correct. In the present study abundances of Coleoptera were significantly higher in winter compared to the other seasons, while their species richness peaked both in winter and spring.

In arid regions, rainfall acts on emergence patterns, the oviposition, egg development and juvenile survival of insects (Milton & Dean 1992; Gebeyehu & Samways 2006a, b). In the Succulent Karoo, adults of Hemiptera: Cicadidae, whose nymphs live below ground feeding on plant roots, emerged two weeks after the late spring rains (Milton & Dean 1992). Abundances of grasshoppers (Orthoptera) were sensitive to inter-annual changes in rainfall, with peaks in abundances during the rainiest year (Gebeyehu & Samways 2006b). In the desert bee *Perdita portalis* (Hymenoptera: Apoidea), emergence patterns occur in synchrony with the late summer rains (Danforth 1999). During the rainy seasons, most pollinators use the same cues that influence flowering as emergence cues and in particular rainfall has been found to be an important cue (Whitehead 1984; Struck 1994a). In the present study, winter was a rainy season. The increased moisture content could have also acted as a cue for emergence of most species in late winter with peaks in spring (Wolda 1988; Paini 2004) thereby increasing abundances and richness of most of the species.

4.4.2 Land use effects.

Species richness and abundance

Leaf litter and litter moisture content have been found to increase richness of detrivores, predators and parasitoids (Moreno *et al*. in press), while their changes in abundances were related to land use, with a decrease in forests with heavy logging compared to conservation forests. Besides changes in detritus, changes in parasitoid assemblages have been shown to follow that of their hosts (Hilszczański *et al*. 2005), increasing with increasing abundances of hosts. These trends were observed in the present study, with lightly grazed sites having increased richness and abundances of parasitoids, such as Scolebythidae, Tachinidae, Bethylidae, scavengers/ fungivores (Sciaridae), predators (Staphylinidae) and herbivores (Fulgoridae and Pentatomidae) (Scholtz & Holm 1985) in winter and spring. The mixed feeders such as Muscidae and specialists including the host-specific Cecidomyiidae and the fungus feeding Mycetophilidae (Scholtz & Holm 1985; Picker *et al*. 2004) were also found in these sites. The pollinator family Megachilidae (Struck 1994a), which were significantly more abundant in lightly grazed

sites in summer are also known to be oligolectic (depending on one or a few plant species) (Paini 2004). The specialist Lepidoptera families Noctuidae, Lycaenidae and Pieridae (Scholtz & Holm 1985) were found to be abundant in the lightly grazed sites during the wetter seasons. These could be because the vegetation structural complexity in lightly grazed sites provides habitats for most of the lower trophic levels taxa which are hosts for the higher trophic taxa such as parasitoids. Though not measured, the lightly grazed sites, followed by heavily grazed had much more litter and this together with increased moisture content of the litter in winter and spring could provide more resources for these guilds. The increased predation in lightly grazed sites could be related to the fact that a large number of specialised taxa were found in these sites. Vegetation structure has been shown to be important for herbivorous Orthoptera (Gebeyehu & Samways 2006b). In the case of grasshopper species *Orthochtha dasycnemis*, vegetation structure plays a major role in determining its distribution. This species prefers long green grasses and uses these for the background camouflage against predators and for food (Gebeyehu & Samways 2002; Gebeyehu & Samways 2006b; Samways 2006). Habitat specializations are also common in butterflies, with these preferring certain plant species for in oviposition and nectar sources (Koh *et al*. 2004).

Herbivorous taxa such as Cicadellidae and Agromyzidae were abundant in heavily grazed sites in summer and autumn (Scholtz & Holm 1985). Most of the taxa abundant in heavily grazed sites tend to be those with a wide variety of food preferences. Members of the fly families Calliphoridae, Sciaridae, Phoridae and Coleoptera family Nitidulidae can be predators, scavengers, herbivores and saprophytes (Weaving 2000). These results compare with those of Seymour & Dean (1999) in which abundances of Hemiptera were high in heavily grazed sites at two of the three sampling sites. However, Dennis *et al*. (1998) and Gibson *et al*. (1992) found heavily grazed sites to have low abundances and richness. Their studies were done in grassland ecosystems and it might be possible the mechanisms underlying such ecosystems differ from those in arid areas. They did determine that the herbivorous Homoptera and leaf miners were not only sensitive to plant architecture but also to plant species composition.

Again, in heavily grazed sites, abundance of the pollinator family Fideliidae (Struck 1994a) in summer and autumn was higher. Whitehead (1984) outlined the biology and flower relationships of Fideliidae. Members of this family are ground-nesting (Scholtz & Holm 1985; Whitehead 1984), with population increase and emergence taking place in spring or in summer depending on species. These bees are also known to have very high host plant specificity (Whitehead 1984). In this study, only one species of Fideliidae was trapped in the three land use types, but more abundant in heavily grazed sites, its host plants is therefore likely more abundant in heavily grazed sites. Among the host plants outlined by Whitehead (1984), members of the genera *Arctosis*, *Zygophyllaceae*, *Aridaria* and *Hermannia* were found in the grazed sites, with *Hermannia amoena* Dinter being the only species in the genus *Hermannia* dominating the cultivated sites.

Herbivorous Cicadellidae and Agromyzidae were also abundant in cultivated sites in summer and autumn (Scholtz & Holm 1985). The cultivated sites in this study were dominated by an unpalatable plant species *Galenia africana* L. (Aizoaceae). This dominance could have lead to marked increase in abundance of species that use these plants for food sources, shelter or breeding sites. In desert grassland of Arizona, Butt *et al*. (1980) found that abundance of herbivorous taxa was correlated with annual herb cover and cover of plants which were characteristic of disturbed areas. Also, they found that the dominance of many herbivore taxa during succession were characteristic of disturbed areas. The cultivated sites are also seen to support quite a number of pollinator species throughout the seasons. Scarabaeidae: Hopliini were significantly more abundant in spring while species richness of Bombyliidae and Buprestidae were higher in summer. In autumn, pollinators in the families Anthophoridae, Melittidae and Sphecidae were more abundant (Struck 1994a, b). Some pollinator species, e.g. some species in the family Sphecidae, are known to form nests from burrows excavated in the ground (Picker *et al*. 2004). The high abundance of these pollinators in autumn in cultivated sites could therefore be a result of preference of bare ground for nesting purposes. Spring results were influenced by the occurrence of annual plants, which are known to be pollinated mostly by members of Hopliini group (Struck 1994a). It has been indicated that for pollinator species, selection of plant species that provide rewards such as pollen and

nectar together with areas ideal for nesting and mating are of utmost importance in habitat selection (Kevan & Baker 1999; Kevan & Baker 1983). In bees (Hymenoptera: Apoidea), species diversity is dependent on a number of factors such as the understorey flowering vegetation and the degree of bare ground available for nesting sites (Cody *et al*. 1977). In California, Brown (1987) has shown that diversity of Lepidoptera pollinators is highly correlated to floral diversity. He suggested that this is because the Lepidoptera are highly host specific and that any changes in the floral composition may lead to shifts in their assemblages.

Southwood *et al*. (1979) determined that plant and invertebrate dynamics during succession in fallow fields seem to depend on the stage of succession. The author found that up to a succession age of sixteen months, the taxonomic diversities of plants and insects (Heteroptera and adult Coleoptera) rose, thereafter the diversity of plant species declined while that of insects remained fairly constant. Dean & Milton (1995) found the abundance of the Homoptera, Orthoptera, Coleoptera and Hymenoptera: Apoidea and wasps (Hymenoptera) was highest in the 30 year old fallow field compared to an undisturbed field and 17 year fallow field. In the present study the fallow field was last cultivated in 1977, making it 30 years fallow. Similar to Dean & Milton (1995), Homoptera and pollinators were more abundant in these fallow fields, indicating that the dynamics of the cultivated field in the present study are similar to Dean & Milton's (1995) findings. A striking finding by Southwood *et al*. (1979), which is also very similar to what we found, is that the invertebrate community of the disturbed sites shows a promise of attaining levels of similarity with lightly grazed sites, which can be considered relatively pristine in this case, even though the plant communities are very different to what they were before disturbance.

One other possible reason for the increased abundances of pollinator species in cultivated field could be that these insects are attracted to yellow masses of *G. africana* in these fields. Because of high cover of this species in cultivated fields, the cultivated field display yellow masses during the dry seasons and changes somewhat green-yellow during the rainy seasons. Insects are known to use visual, chemical and tactile cues in

location of their host plants (Atkins 1980; Edwards & Wratten 1980), with their visual spectrum ranging from 300nm (ultraviolet) to 650nm (yellow-orange) (Kevan & Baker 1983). The female tobacco hornworms *Manduca sexta* (Lepidoptera) use vision to detect their host plant while odour determines landing (Edwards & Wratten 1980). Yellow is known to attract an unlimited number of insects (Kevan & Baker 1999; Kevan & Baker 1983; Proky & Owens 1983; Edwards & Wratten 1980), including Aphididae and Hemiptera, certain Coleoptera and Apoidea (Atkins 1980; Kevan & Baker 1983). Their response to the colour of vegetation seems to play an important part in food location but not in discriminating the host plant (Atkins 1980). In Aphididae, there is no specific host finding behaviour but these pests seem to be attracted to yellow plants and prefer plants conspicuous against bare ground (Edwards & Wratten 1980). In the Succulent Karoo, Mayer *et al.* (2006) found most species of Hopliini to be highly attracted to yellow flowers.

Besides this dominance by *G. africana*, the cultivated field also had a lot of bare ground. Aphididae, members of Pieridae and whiteflies (Aleyrodidae) were found to respond more to host plants surrounded by bare ground than those surrounded by weeds (Smith 1976). In ovipositing Lepidoptera of the genus *Battus*, a host plant that was surrounded by vegetation was less visible than that surrounded by little or no vegetation (Rausher 1981). Hence, the high abundances and richness of flying invertebrates in the cultivated fields could be a result of the yellow colour of the dominant plant species and bare area that affords good contrast for the plants, as well as nesting sites for ground nesting species. In this regard, a disturbance indicator; *G. africana* (Todd & Hoffmann 1999) that is otherwise unpalatable to livestock (Simons & Allsopp 2007) could have an effect on the assemblages of the flying invertebrates, yet this remains largely to be determined.

Assemblages

In this study, the cultivated and lightly grazed sites had high abundances of nectar and pollen feeding taxa that act as pollinators. The dominant perennial plant species in cultivated sites was *G. africana* and this together with bare ground in the drier summer

and autumn months influenced the assemblages in these sites. The lightly grazed sites with higher percentage cover of succulent plant species and rock cover supported very different assemblages from the cultivated and heavily grazed sites. Spring and winter were typified by most of the bare ground replaced by annual plant species in heavily grazed and cultivated fields. ANOSIM gave strong differences between land uses in all seasons except winter, and the differences between cultivated and lightly grazed sites were found to be highest (SIMPER). The RDA results show that the environmental characteristics can be attributed to the assemblages. These results show that vegetation differences between areas of different land use can be attributed to the differences in assemblages, similar to what other studies have found (Neff *et al*. 2007; Mayer 2005; Vohland *et al*. 2005; Rambo & Faeth 1999). Changes in plant composition have also been demonstrated in the Succulent Karoo under different land uses (Hoffman & Cowling 1990; Milton *et al*. 1994). The results were specific for taxa, as for example, the significantly high abundances of monkey beetles in cultivated and lightly grazed sites in spring. These results are similar to those obtained by Vohland *et al*. (2005); Colville *et al*. (2002). The high abundance of these important pollinators (Picker & Midgley 1996), known to be host specific (Picker & Midgley 1994) could have been a result of high abundances of host plants, a trend that was observed by Mayer (2005) where she found the diversity, richness and abundances of bees to be higher with high flower abundances.

Indicator species

The dominance of cluster Dendograms by samples from Kleinfontein and Kuile shows that besides the land use effects, the geographic location also plays a role in determining assemblages. Seymour & Dean (1999) also found the same results. However, because of the flexibility of Dufrêne & Legendre (1997) method, which uses both uniqueness of a species to sites of a particular land use as well as the spread within such sites (McGeoch & Chown 1998), indicators for land use could still be identified. With the exception of only two species, indicators differed between the seasons for each land use. Almost all species that were identified as indicators contribute to the dissimilarity between land uses, and they are also displayed on RDA plots being closely associated with sites for which they are indicators. Colville *et al*. (2002) outlined that the use of individual species

and guilds as indicators in studies where an entire range of unrelated invertebrate taxa have been used to monitor disturbance is not possible. The results they obtained for using monkey beetles as indicators proved the monkey beetles to be ideal as indicators because disturbed and undisturbed supported different assemblages of monkey beetles. Indeed in the present study, two species of monkey beetles were found to be indicators for cultivated sites and one species for the lightly grazed sites.

In conclusion, the flying invertebrate assemblages in the Succulent Karoo change seasonally, mainly because of climatic conditions and between land use types due to changes in vegetation composition and structure. These seasonal changes are seen at order, guild and even species levels. Lightly grazed sites support taxa that are specialized and pollinators, while the heavily grazed sites support most of the mixed feeders. The cultivated sites support high abundances and richness of herbivores and pollinators, probably because of the yellow display of *Galenia africana* L. and the bare ground which is favoured by ground nesting taxa.

4.5 Implications for management

Evidently, the two most common agricultural practices; grazing and cultivation in the Succulent Karoo have transformed the biome's landscape. Abandoned previously cultivated fields bear monotonous landscapes that are dominated by disturbance tolerant plant species that are non palatable to livestock. Although grazing can be compatible to maintenance of biodiversity, overgrazing on the other hand has degraded the area, also leading to changes in plant species composition and structure.

This study shows that the lightly grazed sites bear the highest vegetation structural diversity. Plant species composition is also higher in these sites. These sites evidently bear the high diversity of vegetation associated invertebrates, and this cascades up the feeding guilds, in which higher guilds such as parasitoids were found in these sites. However, this was only during the wetter part of the year. A lot of invertebrate functional groups were found in these sites during these seasons are clearly the result of availability

of resources for most of the invertebrates. With this, a lot of higher taxa species increase with increase in their prey numbers.

Vegetation structural complexity and composition are lost is the heavily grazed sites and very minimal in previously cultivated fields. These sites tend to have the highest seasonal vegetation changes, with sprouting of annual plant species after the winter rains. Results of grazing are evident, as in the case of increased bare ground in these sites. Slow succession rates in fallow fields also lead to these fields having high cover of bare ground. However, there were taxa such as Fideliidae which preferred only the heavily grazed sites. Cultivated sites harboured most of the pollinators, and herbivores during autumn and spring. These results are therefore not entirely conclusive and show that the lightly grazed, heavily grazed and cultivated site all have value in conservation of the flying invertebrates in the Succulent Karoo.

This implies that for conservation purposes, the highest richness of flying insects could be attained by having a mosaic of different land uses as these tend to have differing communities. According to Mayer *et al*. (2006), these would provide a pool of insect movement from one land use type to the next. Also, considering that location also plays a major role in structuring assemblages, conservation initiatives should also focus on specific localities. Dufrêne & Legendre (1997) method of classifying indicators becomes very useful in these regard, as it can identify areas of best conservation value, depending on how species are associated with such localities.

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APPENDIX 1.

Total abundance of flying insects caught in pan traps per land use type per season..Only species with total abundance of five and more individuals per season shown.

Order	Species	Abrev	Summer			Autumn			Winter			Spring		
			CL	HG	LG	CL	HG	LG	CL	HG	LG	CL	HG	LG
Coleoptera	Chrysomelidae sp.1	Chry1											6	8
Coleoptera	Chrysomelidae sp.13	Chry13										1	9	3
Coleoptera	Chrysomelidae sp.7	Chry7							19	169	184			
Coleoptera	Cleridae sp.1	Cle1											17	148
Coleoptera	Coccinellidae sp.2	Coc2	4		2	1								
Coleoptera	Coleoptera sp.1	Col1											1	76
Coleoptera	Coleoptera sp.10	Col10										4	6	
Coleoptera	Curculionidae sp.2	Curc2				5	6	6					3	
Coleoptera	Curculionidae sp.9	Curc9	28	29	17							2	6	1
Coleoptera	Meloidae sp.11	Melo11										12		
Coleoptera	Meloidae sp.7	Melo7										5	5	
Coleoptera	Meloidae sp.8	Melo8										116	38	32
Coleoptera	Mordellidae sp.3	Mor3				12		1			3			
Coleoptera	Mordellidae sp.4	Mor4											7	
Coleoptera	Nitidulidae sp.1	Nit1											41	9
Coleoptera	Nitidulidae sp.11	Nit11	1					1	73	349	245	11	68	50
Coleoptera	Nitidulidae sp.12	Nit12							25		25	23	89	53
Coleoptera	Nitidulidae sp.14	Nit14	5	4		29	1	2	137	179	250	8	17	14
Coleoptera	Nitidulidae sp.15	Nit15										17	9	18
Coleoptera	Nitidulidae sp.5	Nit5	1			4			43	42	65	8	22	30
Coleoptera	Nitidulidae sp.6	Nit6				1			7	10		8	7	1
Coleoptera	Nitidulidae sp.7	Nit7				1		3	50	3			15	
Coleoptera	Nitidulidae sp.9	Nit9					2		13	318	226	48	17	39
Coleoptera	Pselaphidae sp.1	Pse1												16
Coleoptera	Scarabaeidae sp.10	Sca10							25	8	8	1		1
Coleoptera	Scarabaeidae sp.11	Sca11								2	18	3	1	1
Coleoptera	Scarabaeidae sp.16	Sca16								1		64	42	131
Coleoptera	Scarabaeidae sp.17	Sca17										16	17	49
Coleoptera	Scarabaeidae sp.18	Sca18										4		1
Coleoptera	Scarabaeidae sp.19	Sca19										35		1
Coleoptera	Scarabaeidae sp.2	Sca2											2	8
Coleoptera	Scarabaeidae sp.20	Sca20										6	4	
Coleoptera	Scarabaeidae sp.21	Sca21										6	2	4
Coleoptera	Scarabaeidae sp.23	Sca23										25	2	6
Coleoptera	Scarabaeidae sp.24	Sca24										20	2	7
Coleoptera	Scarabaeidae sp.25	Sca25										8	3	
Coleoptera	Scarabaeidae sp.27	Sca27										9		6
Coleoptera	Staphylinidae sp.7	Sta7											1	6
Total abundance			**39**	**33**	**19**	**53**	**9**	**13**	**392**	**1081**	**1024**	**460**	**459**	**719**
Diptera	Agromyzidae sp.1	Agr1				3	5							
Diptera	Agromyzidae sp.10	Agr10					14	2						

Order	Species	Code												
Diptera	Agromyzidae sp.13	Agr13				8								1	
Diptera	Agromyzidae sp.14	Agr14		4	16			6					1	2
Diptera	Agromyzidae sp.19	Agr19								6	2				
Diptera	Agromyzidae sp.2	Agr2			1	4	1		98				2	1
Diptera	Agromyzidae sp.20	Agr20	3									5	18	10
Diptera	Agromyzidae sp.21	Agr21										5		
Diptera	Agromyzidae sp.24	Agr24											1	6
Diptera	Agromyzidae sp.3	Agr3				4	5							
Diptera	Agromyzidae sp.5	Agr5				1	8	1						
Diptera	Agromyzidae sp.6	Agr6	4	23	4	5	24	14						
Diptera	Anthomyidae sp.1	Antho1											9	3
Diptera	Anthomyidae sp.2	Antho2	1			9	3	2	6	2	1	1	9	1
Diptera	Asilidae sp.3	Asi3								2	3		9	8
Diptera	Bibionidae sp.2	Bib2										1	9	1
Diptera	Bombyliidae sp.12	Bom12	1		1	6	2	1						
Diptera	Bombyliidae sp.15	Bom15				1	1	1	11		1			
Diptera	Bombyliidae sp.16	Bom16	12	2	2		1	2						
Diptera	Bombyliidae sp.19	Bom19						16						
Diptera	Bombyliidae sp.20	Bom20						1	5		5			1
Diptera	Bombyliidae sp.23	Bom23	4	20	26	822	237	613					1	2
Diptera	Bombyliidae sp.24	Bom24							13	1	1			
Diptera	Bombyliidae sp.25	Bom25							134	97	258	12	32	17
Diptera	Bombyliidae sp.26	Bom26							3		6			
Diptera	Bombyliidae sp.7	Bom7												7
Diptera	Bombyliidae sp.8	Bom8												6
Diptera	Calliphoridae sp.3	Cal3				3	10	2	1	2	1	2	12	1
Diptera	Cecidomyiidae sp.4	Cec4									1		3	4
Diptera	Chironomidae sp.2	Chi2								7			1	
Diptera	Chloropidae sp.12	Chl12											10	10
Diptera	Chloropidae sp.3	Chl3	15		6	1	3	1						
Diptera	Chloropidae sp.8	Chl8			1	5	3							
Diptera	Chloropidae sp.9	Chl9		4	2					3	1			
Diptera	Drosophilidae sp.2	Dro2			2	2				3	1	3	19	13
Diptera	Drosophilidae sp.4	Dro4					7	6						
Diptera	Empididae sp.1	Emp1				6								
Diptera	Empididae sp.10	Emp10				1	1	4	3	4	2			
Diptera	Empididae sp.11	Emp11					2		23	16	15	5	51	18
Diptera	Empididae sp.14	Emp14						16	2					
Diptera	Empididae sp.18	Emp18										13	41	18
Diptera	Empididae sp.20	Emp20											25	10
Diptera	Empididae sp.5	Emp5	1	3		6			8	10	1	3	1	12
Diptera	Empididae sp.7	Emp7				3		3	2					
Diptera	Fannidae sp.1	Fan1	5		1	2		1					2	
Diptera	Fannidae sp.3	Fan3	2						3	2	8	1		
Diptera	Milichiidae sp.2	Mil2	13	9	1		1	2						

Order	Taxon	Code												
Diptera	Milichiidae sp.3	Mil3	1									3	133	92
Diptera	Milichiidae sp.4	Mil4											179	123
Diptera	Muscidae sp.10	Mus10					4	1		2	6			2
Diptera	Muscidae sp.16	Mus16	14	43	75	10	43	75	2	9	33	1	10	12
Diptera	Muscidae sp.3	Mus3				7	1	1			6		2	
Diptera	Muscidae sp.5	Mus5				2	2	23		1	3	2	1	19
Diptera	Muscidae sp.7	Mus7	8	14	50	4	7	17			3	3	4	
Diptera	Mycetophilidae sp.1	Myc1				1				11	17		4	21
Diptera	Mycetophilidae sp.2	Myc2							114	9	8		93	33
Diptera	Mycetophilidae sp.3	Myc3									8			
Diptera	Mycetophilidae sp.4	Myc4								40	3			
Diptera	Rhagionidae sp.2	Rha2			1		3			14	36			
Diptera	Rhagionidae sp.6	Rha6										5		
Diptera	Sarcophagidae sp.3	Sar3	1	1				5	1			1	12	5
Diptera	Scenopinidae sp.2	Sce2				275	2	322	2	3	1			
Diptera	Scenopinidae sp.3	Sce3									8	1		
Diptera	Sciaridae sp.1	Sci1												5
Diptera	Sciaridae sp.5	Sci5	4		2					39	20	11	2249	120
Diptera	Sepsidae sp.2	Seps2										4		1
Diptera	Tabanidae sp.4	Tab4		5	5	3	1						2	
Diptera	Tachinidae sp.12	Tac12							4	1		1		
Diptera	Tachinidae sp.14	Tac14	1			5	1	1						2
Diptera	Tachinidae sp.15	Tac15				13	2	1				26	2	4
Diptera	Tachinidae sp.8	Tac8				6	25	15			3	1	1	2
Diptera	Tachinidae sp.9	Tac9				3	3	1			1		2	
Diptera	Tephritidae sp.14	Tep14											2	5
Diptera	Tephritidae sp.2	Tep2	1			2	9	1	1	6	1	4	5	2
Diptera	Tephritidae sp.3	Tep3							7				1	2
Diptera	Tephritidae sp.4	Tep4							5	13	14	1		
Diptera	Tephritidae sp.7	Tep7	7	1	1							2	1	
Diptera	Therevidae sp.10	The10	4			62	5	34	3			110	84	19
Diptera	Therevidae sp.11	The11	2	5	3							203	104	10
Diptera	Therevidae sp.12	The12										4	7	3
Diptera	Therevidae sp.13	The13										6	10	
Diptera	Therevidae sp.4	The4							3	10	14	24	43	29
Diptera	Therevidae sp.7	The7								1	4		5	
Diptera	Therevidae sp.8	The8			1	374	164	935	1			96	42	46
Total abundance			**104**	**134**	**201**	**1659**	**600**	**2126**	**450**	**317**	**478**	**589**	**3249**	**705**
Hemiptera	Cicadellidae sp.1	Cic1											11	
Hemiptera	Cicadellidae sp.10	Cic10						1	36	21	10			
Hemiptera	Cicadellidae sp.12	Cic12			1	9	24		1	9				
Hemiptera	Cicadellidae sp.13	Cic13	1	1		6	7							
Hemiptera	Cicadellidae sp.14	Cic14				12	14	9	21					
Hemiptera	Cicadellidae sp.15	Cic15	2312	236	32	45	179	8	8	9	4	53	13	4
Hemiptera	Cicadellidae sp.17	Cic17				22	1							
Hemiptera	Cicadellidae sp.19	Cic19										29	16	10
Hemiptera	Cicadellidae sp.6	Cic6				2	3	7		3	1			

Order	Species	Code												
Hemiptera	Cicadellidae sp.7	Cic7				12	9			28	3			
Hemiptera	Cicadellidae sp.8	Cic8				16	18	7						
Hemiptera	Cicadellidae sp.9	Cic9				1		5						
Hemiptera	Fulgoridae sp.1	Ful1				9	75	23	1				9	9
Hemiptera	Fulgoridae sp.2	Ful2				4	57	41					4	5
Hemiptera	Miridae sp.8	Mir8										1	3	1
Hemiptera	Pentatomidae sp.3	Pen3				1								6
Total abundance			**2313**	**237**	**33**	**139**	**388**	**100**	**67**	**70**	**18**	**83**	**56**	**35**
Hymenoptera	Anthophoridae sp.1	Anth1				22		12					1	4
Hymenoptera	Anthophoridae sp.2	Anth2				5						1		
Hymenoptera	Anthophoridae sp.3	Anth3				3		2						
Hymenoptera	Anthophoridae sp.6	Anth6	1	5	10	1								
Hymenoptera	Apidae sp.2	Api2	4	16	1	1	5	1				1		
Hymenoptera	Apidae sp.4	Api4					12	6						
Hymenoptera	Bethylidae sp.1	Bet1		1		1	5	4					1	4
Hymenoptera	Braconidae sp.10	Bra10							3	2		7	14	4
Hymenoptera	Chalcididae sp.1	Cha1	1	1	3								1	1
Hymenoptera	Chalcididae sp.9	Cha9	1	1	2					3	2	2		
Hymenoptera	Fidellidae sp.1	Fid1	14	15	5	6	11			1		1	2	3
Hymenoptera	Halictidae sp.1	Hal1	25	29	11								1	
Hymenoptera	Halictidae sp.10	Hal10	94	170	145		13					3		
Hymenoptera	Halictidae sp.13	Hal13				1	1	3						1
Hymenoptera	Halictidae sp.14	Hal14	1		1	49	100	304	5	6	18			
Hymenoptera	Halictidae sp.15	Hal15				3	85			2				
Hymenoptera	Halictidae sp.16	Hal16				14	5	5				1		
Hymenoptera	Halictidae sp.17	Hal17				402	56	99				7	40	11
Hymenoptera	Halictidae sp.18	Hal18				6	24	115				14	37	25
Hymenoptera	Halictidae sp.19	Hal19				29	8	2						1
Hymenoptera	Halictidae sp.20	Hal20				12	14	1		1	5			
Hymenoptera	Halictidae sp.22	Hal22	44	29	19					2	4	3		1
Hymenoptera	Halictidae sp.23	Hal23	24	15	5							1		
Hymenoptera	Halictidae sp.24	Hal24	1									12	2	4
Hymenoptera	Halictidae sp.27	Hal27										16	15	11
Hymenoptera	Halictidae sp.4	Hal4				5								
Hymenoptera	Halictidae sp.7	Hal7	3	5	10	6		3						
Hymenoptera	Halictidae sp.8	Hal8	6	8	2	5	24						1	
Hymenoptera	Halictidae sp.9	Hal9				19	29		1		1	1		
Hymenoptera	Ichneumonidae sp.1	Ich1							3	11	15		1	1
Hymenoptera	Ichneumonidae sp.2	Ich2	1							6			1	
Hymenoptera	Masaridae sp.1	Mas1	5	3									10	3
Hymenoptera	Masaridae sp.11	Mas11				179	8	66				4	3	3
Hymenoptera	Masaridae sp.12	Mas12				26	1	1						
Hymenoptera	Masaridae sp.14	Mas14	1		1	1	4							
Hymenoptera	Masaridae sp.2	Mas2											12	5
Hymenoptera	Masaridae sp.6	Mas6												15
Hymenoptera	Megachilidae sp.1	Meg1			1	11	1	2						

Order	Species	Code												
Hymenoptera	Megachilidae sp.2	Meg2				7		5						
Hymenoptera	Megachilidae sp.3	Meg3	2	1	1	4		5						
Hymenoptera	Megachilidae sp.4	Meg4				21								
Hymenoptera	Megachilidae sp.5	Meg5	1	4	2	39	13	19						
Hymenoptera	Melittidae sp.11	Mel11				19							1	11
Hymenoptera	Melittidae sp.12	Mel12				15							1	
Hymenoptera	Melittidae sp.13	Mel13	82	61	69	29	2	24				2	1	2
Hymenoptera	Melittidae sp.16	Mel16									6	1	2	
Hymenoptera	Melittidae sp.17	Mel17								20	5	3	1	1
Hymenoptera	Melittidae sp.3	Mel3				8		2						
Hymenoptera	Plumariidae sp.2	Plu2	3	15	12									
Hymenoptera	Scolebythidae sp.1	Sco1											1	55
Hymenoptera	Sphecidae sp.12	Sph12				11							2	
Hymenoptera	Sphecidae sp.13	Sph13				13		10					3	2
Hymenoptera	Sphecidae sp.15	Sph15										11		
Hymenoptera	Sphecidae sp.16	Sph16										34	4	9
Hymenoptera	Sphecidae sp.17	Sph17										47		
Hymenoptera	Sphecidae sp.18	Sph18										7	1	1
Hymenoptera	Sphecidae sp.22	Sph22										1	37	46
Hymenoptera	Sphecidae sp.23	Sph23										25		
Hymenoptera	Sphecidae sp.3	Sph3	4	2		23	1							
Hymenoptera	Sphecidae sp.4	Sph4				4		5						
Hymenoptera	Symphyta sp.13	Sym13	2		1								1	9
Hymenoptera	Vespidae sp.2	Ves2			2			1					1	4
Total abundance			**320**	**381**	**303**	**1000**	**422**	**697**	**12**	**54**	**58**	**186**	**226**	**226**
Lepidoptera	Lycaenidae sp.1	Lyc1	3		5	1	3	3						
Lepidoptera	Microlepidoptera sp.19	Mic19	5	2	3									
Lepidoptera	Microlepidoptera sp.2	Mic2	2	1	3				1				5	7
Lepidoptera	Microlepidoptera sp.26	Mic26		2	1	3	21	19	7	1	1		2	1
Lepidoptera	Microlepidoptera sp.3	Mic3		1						1			3	8
Lepidoptera	Microlepidoptera sp.32	Mic32				1	130	18						
Lepidoptera	Microlepidoptera sp.34	Mic34				1	89	47						
Lepidoptera	Microlepidoptera sp.41	Mic41					1	8						
Lepidoptera	Microlepidoptera sp.5	Mic5				5	33	31	1					
Lepidoptera	Microlepidoptera sp.50	Mic50						6						1
Lepidoptera	Microlepidoptera sp.57	Mic57	2									3	10	8
Lepidoptera	Microlepidoptera sp.62	Mic62		2					1		1		1	9
Lepidoptera	Microlepidoptera sp.65	Mic65	5							1		1	4	2
Lepidoptera	Microlepidoptera sp.66	Mic66	10		4									
Lepidoptera	Microlepidoptera sp.67	Mic67											6	
Lepidoptera	Microlepidoptera sp.7	Mic7									1		5	2

Order	Species	Code												
Lepidoptera	Microlepidoptera sp.70	Mic70	1	3	3							6	3	7
Lepidoptera	Microlepidoptera sp.71	Mic71	71	16	17								1	1
Lepidoptera	Microlepidoptera sp.74	Mic74	96	20	13	57	185	16	8			4	1	
Lepidoptera	Noctuidae sp.6	Noc6					2					2	9	6
Lepidoptera	Nymphalidae sp.1	Nym1					3		9	10			1	1
Lepidoptera	Pieridae sp.5	Pie5					4	1	25					
Total abundance			**195**	**47**	**49**	**77**	**463**	**173**	**27**	**13**	**3**	**16**	**51**	**53**
Orthoptera	Acrididae sp.3	Acr3					1	6						
Total abundance			**0**	**0**	**0**	**0**	**1**	**6**	**0**	**0**	**0**	**0**	**0**	**0**
Psocoptera	Psocoptera sp.4	Pso4				8	3			3	14			5
Total abundance			**0**	**0**	**0**	**8**	**3**	**0**	**0**	**3**	**14**	**0**	**0**	**5**
Overall abundance			**2971**	**832**	**605**	**2936**	**1886**	**3115**	**948**	**1538**	**1595**	**1334**	**4041**	**1743**
Seasonal abundance			**4408**			**7937**			**4081**			**7118**		
Grand total abundance			**23544**											

APPENDIX 2A.
Summary of flying insect mean relative abundances in each of the land use across the seasons. CL = Cultivated sites, HG = heavily grazed sites, LG = lightly grazed sites. Underlined number indicates where relative abundance was highest.

	Autumn			Spring			Summer			Winter		
	CL	HG	LG	CL	HG	LG	CL	HG	LG	CL	HG	LG
Blattodea	---	---	---	---	---	0.1	---	0.1	0.3	---	0.1	0.1
Coleoptera	2.1	0.8	1.2	31.7	11.4	37.3	1.7	6.6	3.9	38.4	67.3	62.8
Dermaptera	---	---	---	0.1	---	---	---	---	---	---	---	0.1
Diptera	53.0	31.8	63.8	44.2	77.3	41.5	4.8	17.4	33.8	49.3	23.8	29.3
Hemiptera	5.2	17.1	3.3	7.0	2.6	3.5	75.3	26.4	5.1	7.3	4.4	1.3
Hymenoptera	33.7	19.7	22.3	14.8	6.5	12.9	11.3	42.8	47.6	1.8	3.4	4.7
Lepidoptera	4.5	30.3	9.1	2.2	2.0	4.1	6.6	6.0	8.6	3.3	0.9	0.5
Neuroptera	---	---	0.1	---	0.1	0.1	0.1	0.1	---	---	---	0.2
Orthoptera	0.1	0.1	0.3	0.1	---	0.2	---	0.1	0.4	---	---	---
Psocoptera	0.4	0.1	---	0.1	0.1	0.4	0.1	0.4	0.4	---	0.2	0.8
Thysanoptera	0.2	0.1	---	---	0.1	---	---	---	---	---	---	0.2

APPENDIX 2B.
Summary of flying insect species richness in each of the land use across the seasons. CL = Cultivated sites, HG = heavily grazed sites, LG = lightly grazed sites. Underlined number indicates where the number of species was highest.

	Autumn			Spring			Summer			Winter		
	CL	HG	LG	CL	HG	LG	CL	HG	LG	CL	HG	LG
Blattodea	---	---	---	---	---	2	---	1	1	---	1	1
Coleoptera	18	13	15	52	57	70	16	14	9	14	117	17
Dermaptera	---	---	---	1	---	---	---	---	---	---	---	1
Diptera	77	69	67	86	98	102	43	28	29	40	44	54
Hemiptera	22	16	12	16	25	24	18	13	5	8	9	8
Hymenoptera	75	45	63	63	62	55	46	41	46	9	13	23
Lepidoptera	35	34	38	13	27	27	14	15	15	11	6	7
Neuroptera	---	---	1	---	1	1	1	1	---	---	---	1
Orthoptera	2	1	3	1	---	3	---	1	3	---	---	---
Psocoptera	3	1	---	1	2	3	3	2	3	---	1	1
Thysanoptera	1	1	---	---	1	---	---	---	---	---	---	1

CHAPTER 5. GENERAL DISCUSSION AND CONCLUSION

Overgrazing by domestic livestock is considered as one of the major causes of land degradation and the biggest threat to the biodiversity of the Succulent Karoo (Hahn *et al.* 2005), especially in communal areas, where large numbers of livestock are kept (Riginos & Hoffman 2003). This leads to changes in vegetation composition and structure (Anderson & Hoffman 2007). Compositional shifts include changes in growth form from perennial plant species to annual plant species (Todd & Hoffman 1999) and shifts from large succulents and woody shrubs to non succulent dwarf shrubs and ephemeral herbs, annuals, geophytes and unpalatable plant species (Todd & Hoffman 1999; Anderson & Hoffman 2007). After cultivation, abandoned fields undergo succession pathways that vary in species richness and composition (Dean & Milton 1995; Bonet 2004) and such fields have been shown to take many decades to re-establish (Dean & Milton 1995). This study has also shown vegetation changes in composition and structure in the different land use types; grazing at different intensities and cultivation. Abandoned fields harbour the lowest number of plant species, and these together with the heavily grazed sites have a high cover *Galenia africana* L. which is unpalatable (Riginos & Hoffman 2003). Lightly grazed sites have the highest vegetation structural complexity, with a high cover of both dwarf and shrub succulents as well as non succulent perennials. After the winter rains, annual plants occupy most of the bare ground in heavily grazed and previously cultivated sites.

Our study has shown that these vegetation changes are reflected in changes in invertebrate species numbers and abundances in the different land use types. Hymenoptera: Formicidae were the greatest contributors to ground-dwelling invertebrate assemblages. Overall, grazing and cultivation in the Succulent Karoo led to a skewed community composition of ground-dwelling invertebrates which favour disturbance-tolerant and generalist species such as *Anoplolepis steingroeveri* (Forel). Most generalist taxa are known to prefer disturbed sites as they are unable to successfully compete with an increasing number of predators such as spiders (Arachnida: Araneae) and ponerine ants (Formicidae: Ponerinae) at less disturbed sites (Dean & Milton 1995; Tshiguvho *et*

al. 1999; Netshilaphala *et al*. 2005). In contrast, less disturbed sites favour more specialised species. The high vegetation complexity on the lightly grazed sites provides resources for specialised species which subsequently cascades down the trophic levels.

Besides Formicidae, other taxa that contributed considerably to ground-dwelling invertebrate assemblages are Araneae and Coleoptera (Tenebrionidae and Carabidae), both in terms of abundance and species numbers. These taxa showed both seasonal and land use type effects (chapter 3). However, very few species of ground-dwelling invertebrates showed significant responses to land use types as opposed to seasonal effects. Araneae and Tenebrionidae were the only taxa that were negatively impacted in terms of species richness. Tenebrionidae are detritus feeders and are well adapted to living in dry, hot environments (Cloudsley-Thompson 2001). They had higher richness in grazed sites. The conclusion to be drawn from this could be that grazed sites as opposed to cultivated sites support detritivores as a result of their vegetation structural complexity, higher cover and resulting higher amounts of dead plant material on the ground. Araneae are known to nest under stones (Dean 1988). In comparison to the cultivated sites, the grazed sites have a higher rock cover. It is therefore possible that the decrease in number of Araneae species from lightly grazed, heavily grazed and cultivated sites could be both a response to decreasing vegetation structural diversity and decreasing rock cover. However, the high abundances of certain species of Araneae in cultivated sites could be a result of dominance of species which are known to bury their prey in the sand after capture and those which are known to dig into the soil when alarmed (Dean 1988; Dippenaar-Schoeman & Harris 2005).

Formicidae and Araneae were the only ground-dwelling taxa that can be considered as indicators for land use in the Succulent Karoo. Other studies conducted in the Succulent Karoo also found similar results for Formicidae (e.g. Tshiguvho *et al*. 1999). Formicidae can also be regarded as ideal indicators for the restoration of mining sites in this biome (Netshilaphala *et al*. 2005). Araneae have never been considered as ideal land use indicators (but see Dean & Milton 1995); hence this study has expanded the knowledge of ground-dwelling indicator species for the Succulent Karoo. This could suggest that

with increased monitoring of ground-dwelling invertebrates, yet more indicators could be discovered in this hotspot and hence the improved understanding of the ecosystem functions of the area for conservation purposes could be achieved.

Seasonal changes in ground-dwelling assemblages are determined largely by climatic conditions, as well as food availability. Abundance and number of species of Collembola increased with increasing rainfall and humidity patterns. Hot and dry conditions favoured species of Solifugae, Scorpiones, Tenebrionidae and most of the Formicidae species, including *Messor capensis* (Mayr) and *Ocymyrmex barbiger* (Emery). Activity of these taxa increases with temperature (Andersen 1997; Witt & Giliomee 1999; Cloudsley-Thompson 2001) and emergence patterns are also known to increase with temperature, as in the case of Tenebrionidae (De Los Santos *et al*. 2006). Predators such as Carabidae and *Camponotus fulvopilosus* (De Geer) (Hymenoptera: Formicidae) could have increased as a result of increasing prey numbers such as Collembola. Seed harvesters, such as *Tetramorium* species possibly responded to increased seed availability in spring after the winter rains and flowering of most plant species.

Responses of flying and ground-dwelling invertebrates to seasonal climatic conditions were different. The overall species richness and diversity peaked in spring for flying invertebrates while peaks in richness for ground-dwelling invertebrates were in summer, with no difference in overall diversity. Overall abundances for ground-dwelling invertebrates were highest in summer and autumn while there were no observed differences for flying invertebrates in terms of overall abundances. The responses however vary, depending on the species in question or species functional groups (Andersen 1986; Hoffmann & Andersen 2003). This therefore demonstrates that invertebrates have varied responses to climatic changes, and an understanding of such changes can be of utmost importance in the Succulent Karoo, where much debate on whether the observed vegetation changes are due to land use effects or due to climatic conditions is of major concern (see Dean *et al*. 1995).

The flying invertebrate assemblages are composed largely of Diptera, Hymenoptera, Coleoptera, Hemiptera and Lepidoptera across all seasons. Seasonal changes were also mainly a result of climatic changes. Species richness and abundances were lowest in winter, though results for abundances were not significant between seasons. This reduction in activity can be attributed to diapause and reduced flight and forage activities for most flying insects during the cold conditions (Struck 1994; Davis *et al*. 2000), which in turn result in reduced abundances and richness. The warmer seasons favour certain taxa, such as Lepidoptera whose activities and life cycle depend on high temperatures (Goodwin & Danthanarayana 1984). Rainfall results in changes in vegetation structure and composition, with annuals sprouting soon after the winter rains and most plants flowering in late winter and early spring. This increased moisture content together with vegetation changes favour many flying invertebrates, whose emergence patterns seem to be highly synchronised with available food resources from sprouting and flowering plants, as in the case of the pollinator taxon, monkey beetles (Coleoptera: Hopliini).

More of the flying invertebrate taxa responded to land use types than ground-dwelling invertebrate taxa. As in ground-dwelling taxa, the general trend was that a high number of specialists such as Cecidomyiidae, Mycetophilidae, Megachilidae and high guild taxa such as parasitoids (Symphyta) and most fungivores and detrivores occurred on the lightly grazed sites. This is most likely related to the high plant diversity and varied structural composition, coupled with probable increase in litter content. Responses of pollinator taxa to land use types varied between seasons. In autumn and spring, the highest richness and abundances of pollinators were found in cultivated and heavily grazed sites, except Buprestidae and Vespidae, which were exceptionally high in lightly grazed sites during spring. In summer, abundances of pollinators were highest in grazed sites and lowest on the cultivated fields. The Buprestidae, however, were the only taxon with the highest richness in cultivated sites during this season. These responses could partly be due to resource availability at the different land use types. In spring, the increased cover of annual plants in cultivated and heavily grazed sites possibly provided food resources for most pollinators, including the monkey beetles, which are known to feed on pollen and nectar of annual plants (Picker & Midgley 1996). Both Buprestidae

and Vespidae are important pollinators of Asteraceae and Mesembryanthemaceae (Struck 1994), with Vespidae showing a high degree of specificity to host plants. The heavily grazed sites had an increased cover and richness of members of these families and their flowering was in spring. This could have provided more resources for these pollinator families.

Similarities in number of species and abundances for pollinator taxa in heavily and lightly grazed sites can be attributed to similarity in plant species richness in these sites. In a recent study by Mayer *et al*. (2006), similar results in terms of species richness were found for monkey beetle assemblages of heavily grazed and lightly grazed sites in the Succulent Karoo. While Mayer *et al*. (2006) determined that species richness for this taxon were similar between these areas of different grazing intensity, the overall abundance of the beetles was higher in heavily grazed sites, quite the opposite of what was found in this study. Instead, the present study revealed high abundances in cultivated sites compared to lightly grazed sites. Mayer *et al*. (2006) emphasised however that despite similarities in species richness, assemblages between land use types were different, since the plant species composition in heavily grazed and lightly grazed sites were different, and attracted different species of monkey beetles. Rarer species were found to be vulnerable to impacts of grazing and were only found in lightly grazed sites or disappeared completely (Mayer *et al*. 2006). Indeed in the present study, the monkey beetle species composition for cultivated and heavily grazed sites was different from those in lightly grazed sites.

This study revealed surprising results for the cultivated fields. The expectation was that these *Galenia africana*-dominated fields would have the lowest richness and abundance of pollinator and other flying invertebrate species because of their similar mosaic of low structural diversity and monotonous composition, but this was not the case. The yellow masses of *G. africana* in these fields possibly attracted a large number of flying invertebrate species (Kevan & Baker 1999; Kevan & Baker 1983; Proky & Owens 1983), while the absence of rocks could provide ideal nesting sites for ground-nesting taxa (Picker *et al*. 2004), and the high cover of bare ground could act as a background that

makes the yellow *G. africana* more visible to insects as they fly (Smith 1976). However, these conclusions need further testing to establish the real cause of high abundances and richness of pollinators and other flying taxa in cultivated fields.

With very few exceptions, flying invertebrate indicator species differ between seasons for each land use. This study has therefore achieved another important goal; determining spatially and temporally explicit indicators for the three land use types in the Succulent Karoo. The importance of Dufrêne & Legendre (1997) method in identification of indicators has been advocated by McGeoch & Chown (1998) and tested by McGeoch *et al*. (2002). As stated by McGeoch & Chown (1998), this method can delimit sites with species that have the highest indicator values, and which can therefore be used to identify core conservation areas for particular species, even when little is known about their distributional or biological information. For instance, the present study has shown that cultivated sites form the core areas for conservation of Halictidae, Melittidae and Sphecidae, while the grazed sites would form core areas for Halictidae, as has been determined from indicators values obtained in autumn. The information obtained in spring shows that Scarabaeidae and Sphecidae could attain a high conservation status in cultivated sites, Melittidae and other Sphecidae species could be conserved in heavily grazed sites while Bombyliidae, Buprestidae, some species of Scarabaeidae and the specialist taxa could be well conserved in lightly grazed sites. The vegetation structural and composition complexity of these sites plays a major role in providing specific habitats and a lot of resources for specialists. The general conclusion is that the lightly grazed sites have the most vegetation-associated species, because of their increased vegetation structural complexity, which are coupled with a large number of functional types. On the one hand, the conservation value of cultivated and heavily grazed sites can not be overlooked, especially when it comes to pollinator species.Conservation of the area should therefore be directed towards keeping a mosaic of the three land use types to achieve the highest species richness for flying insects.

One other use of the identified indicators can be realised for the Succulent Karoo. These species can be used in monitoring and assessment of the studied sites should they be

conserved, and this can help in determining the conservation success of the area. Based on the findings of this study, more indicator species can be determined for the Succulent Karoo, that could, for instance, measure the level of grazing and restoration successes of heavily degraded areas. Thus, in this study, invertebrates, especially flying invertebrate taxa have been shown to be good indicators of land use in the Succulent Karoo. The findings of this study therefore support the notion that invertebrates are valuable indicators of land use types.

5.1 References

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