The Biodiversity Impacts of Shrub Loss in a Semi-arid Environment: Responses of Arthropods, with Particular Reference to Ants

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I dedicate this thesis to my grandfathers

Frank Green and Rhys Clarke

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ABSTRACT

Environmental stress resulting from factors such as over grazing can have far-reaching effects on an ecosystem. This thesis aimed to increase the understanding of the wider biodiversity impact of stress and disturbance in semi-arid systems. The response of the arthropod community, and in particular the ant community, to changes in vegetation associated with over grazing, including the loss of perennial shrubs, was examined in the Flinders Ranges region of South Australia.

Epigaeic arthropod and ant communities were surveyed at a number of sites to look for correlations between their community composition and broad scale environmental differences among sites. This included a comparison of different habitat types and areas with altered vegetation structure, such as the presence or absence of perennial shrubs, within habitats. More specific studies were then undertaken to determine the most important environmental variables affecting ant and arthropod communities. These included two abiotic factors; structure and shade, and the biotic resource homopteran honeydew.

The structure of the epigaeic arthropod and ant communities did appear to vary in relation to large-scale differences within the plant community. The differences seemed most closely associated with the availability of food resources such as homopteran honeydew and, to some degree, differences in habitat structure, but not plant species richness. Similar patterns were found within the ant community and other arthropod groups at this scale.

At a finer scale, an artificial increase in habitat structural complexity did not elicit a response within the ant community but led to a significant increase in the abundance and species richness of spiders. Shade cover appeared to be more important to the ant community. However, only a small number of species responded through changes in their foraging activity during hot weather and these included both thermophilic and cooler temperature foraging species. In contrast, access to homopteran honeydew on acacia shrubs by a dominant *Iridomyrmex* ant was associated with much higher ant nest density and may have a much larger impact on ant community structure. These results suggest that stress-related changes in vegetation structure have broad implications for biodiversity and ecological function.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Sylvia Clarke

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Environmental stress and disturbance can have significant ramifications for an entire ecosystem. Human induced factors such as an increase in grazing pressure resulting from the introduction of domestic stock and feral herbivores (e.g. Rambo and Faeth 1999), an alteration in fire regimes (e.g. Haydon *et al.* 2000; Bond and Keeley 2005), and habitat restoration efforts such as revegetation (e.g. Newman and Redente 2001) can lead to substantial changes within the plant community. These changes within the vegetation are relatively easy to measure as plants are sessile and, at least for perennial species, relatively long-lived. Yet, other less conspicuous organisms within the environment, such as arthropods, are also likely to be affected by such modifications either directly or indirectly through changes in the plant community. Examining the response of these other groups will provide a greater understanding of the wider biodiversity implications of environmental stress and disturbance.

Arthropods are very closely linked with the plant community. Changes within the vegetation resulting from environmental stress are therefore likely to be readily reflected in this group. Plant species diversity (Siemann 1998; Siemann *et al.* 1998), functional composition (Siemann *et al.* 1998; Koricheva *et al.* 2000) and structural diversity (Marc *et al.* 1999; Morris 2000) are all known to all play a role in structuring arthropod communities. Arthropods consume plant matter as herbivores and detritivores, and play key roles in pollination and seed dispersal, as well as microhabitat development through building tunnels and nests (Miller 1993). Arthropods are also part of, and influence, other trophic levels as they serve as food or hosts, produce honeydew and become dead organic matter, remove waste products, dead organisms and other animals, and are vectors for pathogens (Miller 1993).

As well as their close ties with the plant community and other aspects of ecosystem function, the abundance and tremendous diversity of arthropods in almost all environments (May 1978, 2000) allows measurement of changes in their abundance, species richness and community composition to be made relatively easily. This makes them useful model organisms for assessing the wider biodiversity implications of environmental stress and disturbance and, because of this, they are increasingly being used as 'indicators' of ecological change within an environment (McGeoch 1998; Andersen 1999).

Arthropods have been used to measure various aspects of ecological change and a range of arthropod taxa at a variety of taxonomic levels have been employed in this way. Order level diversity and arthropod community changes at order level have been used (e.g. Bromham *et al.* 1999); however, as insect orders often contain co-existing species with very different life cycles and ecological roles, in many instances it may not be sufficiently sensitive to more subtle ecological changes. For example, the order Coleoptera contains a vast range of biological types including predators, parasitoids, and various specialist herbivore groups, often within a single family. Using changes in species diversity and composition within a specific order or family may often reveal more about ecological change within an ecosystem than lumping these organisms together. Various taxa including spiders (Churchill 1997), grasshoppers (Quinn and Walgenbach 1990; Andersen *et al.* 2001), springtails (Collembola) (Greenslade 1997) and ants (Majer 1983; Greenslade and Greenslade 1984a; Andersen 1990) have been used to measure the ecological response to changes within or among environments.

However, even within an order or family species richness can still be very high. The impracticalities of examining all species level relationships may be overcome by using rankings above species level or by examining guilds or functional groups of species that utilise resources in a similar way. These may even be more insightful than examining individual species. Guilds or functional groups within a particular order have also been used to compare environments. This has been undertaken with ants (Andersen 1990), spiders (Churchill 1997), flies (Hughes *et al.* 2000) and grasshoppers (Quinn and Walgenbach 1990), with some level of success.

As each environment supports a different suite of arthropod groups, the most appropriate group and taxonomic level to measure an ecological response to human induced stress is likely to differ among locations. Each cause of disturbance or ecological change (grazing, fire, mining, etc) is also likely to induce changes in the environment that will affect different groups differentially. It is therefore important to choose the focal group for each situation carefully (Andersen 1999).

To be an effective indicator of ecosystem change, taxa need to meet a number of criteria. As well as being diverse, widespread and functionally important (Majer 1983; Greenslade and Greenslade 1984a), they must also be practical to use, sensitive to environmental change, and provide predictable and interpretable results that give insight into the changes within the ecosystem (Andersen 1990). It is also highly desirable that their response to disturbance or stress reflects that of other groups within the same environment (Pearson and Cassola 1992; Andersen 1999).

Indicators of change within an ecosystem are of interest to ecologists as they can be used to interpret changes taking place in other parts of the ecosystem that may be difficult or time consuming to measure directly. Suitable indicators are also of use to land managers if they can supply information on the probability of degradation and the success or failure of restoration efforts (Whitford *et al.* 1998). It is unlikely that one group of organisms will be closely linked with all aspects of ecosystem function. However, arthropods may form part of a suite of indicators, allowing information to be gathered on which components of an ecosystem have improved or become degraded.

The aim of this study was to explore the wider impacts of ecological change in a semi-arid system, by looking for correlations between, and explanations for, patterns in the epigaeic arthropod community and the plant community associated with human induced environmental stress, in particular the loss of perennial shrubs through over-grazing. It aims to increase the understanding of the connection between plant and arthropod communities by determining which plant community variables (particularly broad scale habitat differences, and at a finer scale; habitat structure, shade and food resources) influence arthropod community composition. It also addresses the similarities in the response of different arthropod groups to changes in these variables.

1.2 Study organisms

Due to the low and unpredictable rainfall in semi-arid environments, changes in weather patterns can often have a much greater influence on populations than biotic interactions (Briese 1982b) and the rate of habitat recovery can be greatly limited (Westoby *et al.* 1989). In these environments it is therefore important to choose taxa that are present in high numbers for most of the time, to ensure that they can be sampled and identified whenever needed. For this reason, perennial vegetation is often used to monitor the response of a semi-arid systems to environmental stress (Whitford *et al.* 1998; Landsberg and Crowley 2004). However, the response of perennial plants may not necessarily be representative of biodiversity more broadly and specific arthropod groups may be just as useful.

Ants are likely to be the most appropriate arthropod group to use to measure an ecological response in semi-arid environments because of their high species richness and abundance (Briese and Macauley 1977; Andersen 1990; Dawes-Gromadzki 1999) and close ties with ecosystem function. They are dominant predators and competitors, and also influencing soil, vegetation, nutrient distribution, seed predation and dispersal (Greenslade and Halliday 1983) in such environments. The proportion of worker ants from each nest actively foraging can vary with environmental change and, as these changes occur without the need for mortality or recruitment, their response to change can be rapid (Andersen 1990).

Ant communities are influenced by a number of environmental variables including; availability of food resources (e.g. Bernstein 1974; Bentley 1976; Briese and Macauley 1981; Wilby and Shachak 2000), microclimate (e.g. Carlson and Gentry 1973; Briese and Macauley 1980; Christian and Morton 1992), and interspecific competition (e.g. Greenslade 1976; Briese 1982a; Fox and Fox 1982). Ant communities have been successfully used to monitor minesite rehabilitation (and other causes of ecological change) (e.g. Majer and Nichols 1998; Andersen *et al.* 2003) and disturbance (reviewed in Hoffmann and Andersen 2003) in a variety of environments.

The taxonomy of Australian ants is still inadequately known at species level, but dividing ants into functional groups or guilds has proved useful in numerous studies (e.g. Andersen 1997b; King *et al.* 1998; Majer and Nichols 1998; Dawes-Gromadzki 1999). Ant functional groups were originally proposed by Greenslade (1978) and later modified by Andersen (1990). Species are divided into groups on the basis of generic placement, their geographical distribution, and their biological and ecological roles (Greenslade and Halliday 1983). Taxa within these functional groups vary in a similar way to climate, vegetation type and level of disturbance. Although the functional group approach was devised to facilitate biogeographical comparisons, the relative abundance of different functional groups were later shown to be sensitive to environmental change and to provide information on the processes behind the change (Andersen 1990). Changes within the habitat principally affect the most dominant ant species, with flow-on effects to members of other functional groups through competition (Greenslade and Halliday 1983) and possibly other less obvious interactions.

Changes in spider community composition have also been used to monitor ecological change (Churchill 1997; Marc *et al.* 1999). Spiders appear to be influenced by various environmental variables including habitat structure (e.g. Greenstone 1984; Scheidler 1990), prey abundance (e.g. Gibson *et al.* 1992) and predation (e.g. Gunnarsson 1996). A small number of studies in Australia have recently begun to examine the relationship between aspects of the plant community and disturbance and spider community composition (Simmonds *et al.* 1994; Woinarski *et al.* 2002; Churchill and Ludwig 2004), including in semi-arid environments (Harris *et al.* 2003). Spiders can also be split into functional groups at the level of family for examining their ecological response to change, as species within a family tend to have similar ecological roles (Churchill 1997).

1.3 Study area

The area chosen for this study was a semi-arid region of the Flinders Ranges in South Australia, a line of eroded mountains and hills running 390km from Crystal Brook in the south and ending in arid gibber plains to the north (Brandle 2001). The study sites were concentrated on the plains and low hills of the Central Flinders Ranges near Oraparinna (Figure 1.1).

Aboriginal people inhabited the area around Oraparinna for thousands of years in a hunter-gatherer lifestyle. From around 1850 the area was used as a grazing property until 1971 when it was declared part of the Flinders Ranges National Park. Changes to the landscape have been the result of roadmaking, mining, sheep grazing and other stock, rabbits and feral goats (Symon 1971). The impact on the vegetation from these factors, and in particular overgrazing, has been severe in some areas, leading to an almost total loss of perennial vegetation. The recovery of the perennial shrub layer is very slow, and has been hampered by the continued high grazing pressure from native and feral animals and a paucity of significant rainfall events to promote recovery (Westoby *et al.* 1989). Recruitment of perennial shrubs was noted after the large rain events in the winter of 1996 and summer of 1997 (Alexander and Naismith 2001), but in recent years rainfall has been well below average (N. De Preu unpublished data).

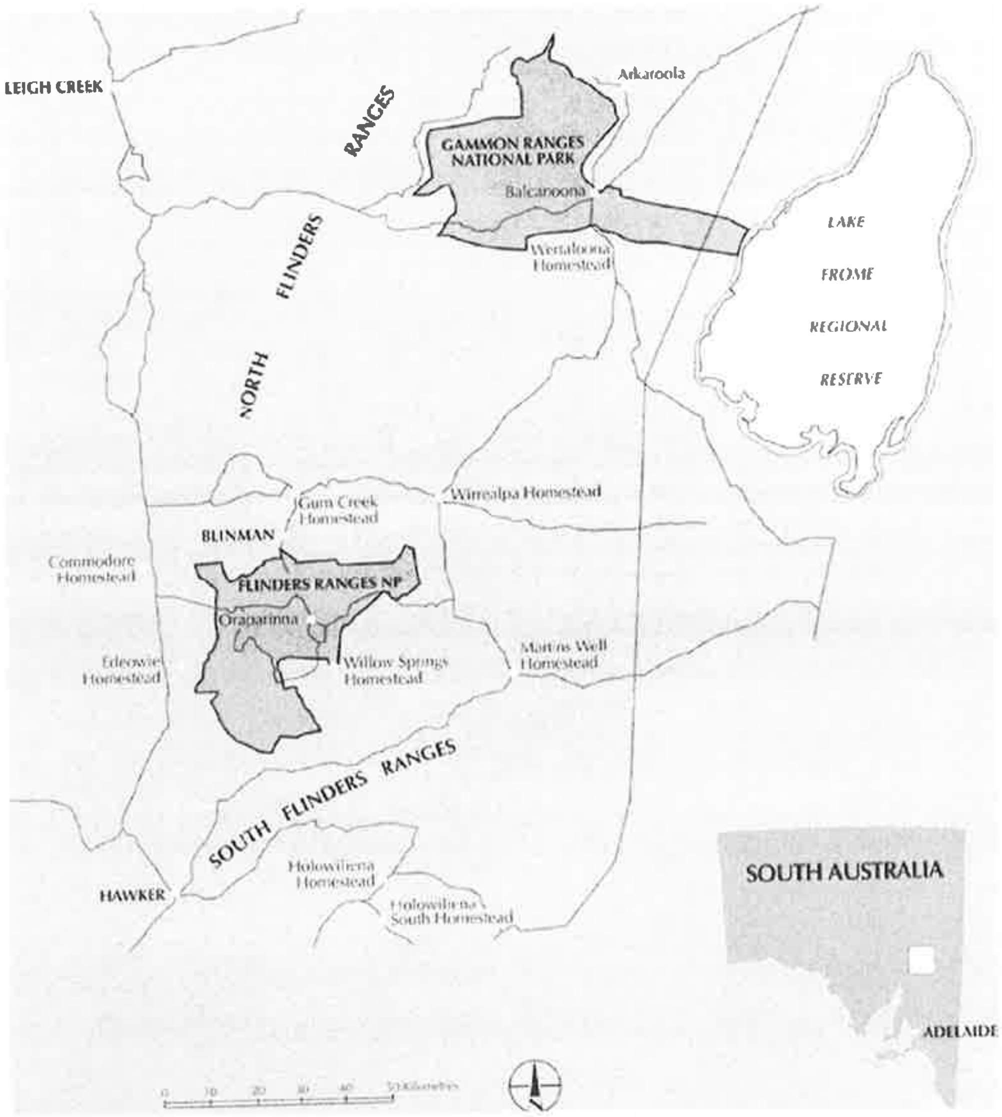


Figure 1.1 Map of Flinders Ranges National Park and surrounding pastoral lease homesteads, South Australia (after Department for Environment, Heritage and Aboriginal Affairs (1999)).

1.4 Organisation of thesis

In this thesis I examine aspects of the ecology of the epigaeic arthropod community and, in particular, the ant and spider communities, and their relationship with the plant community within the semi-arid environment of the Flinders Ranges, South Australia.

While the preceding introduction provides some of the background literature, each chapter is set out as a stand-alone section with an introduction, methods, results and discussion. Most chapters deal with separate studies and although some repetition in explanation of methodologies and information presented within the introductions is unavoidable, it is kept to a minimum.

The first results chapter (Chapter 2) provides details of a pilot study that examined the responses of arthropod assemblages and ant communities to variation in habitat type, as well as grazing, fire and woodland regeneration. Epigaeic arthropods were sampled in a range of habitats (mallee woodland, *Callitris* woodland, spinifex grassland and native grassland) that had been influenced by different causes of ecological change in order to answer the following questions;

- How do arthropod assemblages vary among habitat types?
- How do ant assemblages vary among sites impacted by grazing, fire and woodland regeneration?

As ants were found to be the most diverse and abundant arthropod group and their community composition differed among habitat types and causes of ecological change, they were studied in more detail in Chapter 3. Their response to the loss of shrubs within chenopod shrubland degraded by overgrazing was measured in this case. Their community composition was compared with plant diversity, plant structure and soil condition at sites with and without perennial shrubs. Spiders and wasps were also found to be diverse and abundant within sites and their patterns of species richness were compared with that of the ant communities. Chenopod shrubland was chosen as the vegetation type on which to base the more detailed parts of this study, even though it had not been included in the pilot study, as active restoration programs were being carried out within the National Park and it was hoped the structure of the ant community and knowledge of its connection with the plant community might provide an indication of the success of active and passive habitat restoration efforts. The questions addressed in this chapter were;

- Do areas with and without shrubs support different arthropod and ant communities?
- If so, are these differences correlated with floristic, plant structural or soil condition variables?
- Lastly, do patterns in ant community correlate with patterns in those of other arthropod groups?

Chapter 4 outlines the results of a manipulative experiment designed to simulate the increase in structural complexity that would result from the restoration of an area from ephemeral herbland to chenopod shrubland. Artificial structures were added to plots within the ephemeral herbland using plastic plants of two complexities. This allowed the uncoupling of the abiotic from the biotic effects of an increase in vegetation structure. This chapter outlines the response of the spider and ant communities to the increase in structural complexity. The questions addressed here were;

- Does an increase in structural complexity increase spider abundance and/or species richness in this ephemeral herbland?
- If so, how does the increase correlate with the complexity of the structures?
- Are increases in the abundance and/or species richness of web-building and foliage foraging spider functional groups greater than in other groups?
- Does an increase in structural complexity increase ant abundance and/or species richness in this ephemeral herbland?

A second manipulative experiment, run in parallel with the addition of structural complexity, examined the effect of an increase in shade cover, and is reported in Chapter 5. Shade cover is another factor that changes within plant communities as a result of stress, disturbance and revegetation. Shade tents were installed, each providing approximately the same amount of shade as a bluebush shrub. The effect of this on the ant community was measured after 5 months to answer the following questions;

- Do the foraging patterns of members of the ant community within this environment respond to the addition of shade?
- If so, which groups are most responsive? And what is the optimum shade level for these groups?

Chapter 6 presents the results of a brief investigation into the importance of a biotic resource, homopteran honeydew from acacia shrubs, to a dominant *Iridomyrmex* species. This ant was found to have a very patchy distribution in Chapters 2-4 and, due to its dominance, may be having a large impact on the entire ant community in areas where it is abundant. A comparison of the density of ant nests in areas adjacent to and away from acacia shrubs was made. This chapter attempted to answer the following questions;

- Do *Iridomyrmex* sp. B nests tend to be clustered around the base of *Acacia victoriae* shrubs?
- Do other ant species show any pattern in nest distribution in relation to the shrubs or the *I.* sp. B nests?

A summary of the conclusions from all of the studies and their implications for the broader context of the impact of environmental stress and changes in vegetation on biodiversity in semi-arid systems is provided in Chapter 7.

CHAPTER 2: RESPONSES OF ARTHROPOD ASSEMBLAGES AND ANT COMMUNITIES TO VARIATION IN HABITAT TYPE, GRAZING, FIRE AND WOODLAND REGENERATION IN SEMI-ARID SOUTHERN AUSTRALIA

2.1 Introduction

Terrestrial arthropods are enormously abundant and diverse (May 2000). They are also affected by, and influence, ecosystem function in almost all environments (Miller 1993). It is therefore likely that ecological change will result in alterations in arthropod community structure. The high diversity of terrestrial arthropods makes it impossible, however, to study the entire arthropod community within an environment at species level. The realistic options to measure the response of arthropods to ecological change are therefore to focus on higher taxonomic levels such as orders, or to select a particular group to study in more detail. Order-level diversity and relative abundances have been used to monitor changes within ecosystems (e.g. Bromham *et al.* 1999); however, as insect orders often contain co-existing species with very different life cycles and ecological roles, in many instances order-level analysis is not sensitive enough to detect more subtle ecological changes.

Using changes in species diversity and community composition of a specific order or family may reveal more about ecological change within an ecosystem than would lumping these organisms together. However, even studying species-level changes within an order or family is laborious and is often hindered by taxonomic problems. To overcome this impediment, higher taxonomic levels (e.g. Churchill 1997) and functional groups (e.g. Andersen 1990) are often used, since they provide sufficient information to detect ecological change.

Ants are thought to be ideal arthropod indicators of changes within arid and semi-arid environments (Andersen 1990). They display high diversity and abundance in these environments (Briese and Macauley 1977; Andersen 1990; Dawes-Gromadzki 1999) and are likely to respond to ecological changes as they are numerically and behaviourally dominant predators and competitors, and are closely connected with many aspects of soil, vegetation, nutrient distribution, and seed predation and dispersal (Greenslade and Halliday 1983). Particular ant functional groups have been used to provide a predictive framework for analysing responses of ant communities to disturbance and stress (e.g. Andersen 1997b; King *et al.* 1998; Majer and Nichols 1998; Dawes-Gromadzki 1999).

This chapter reports the results from a preliminary investigation into the epigaeic arthropod assemblages of four habitat types in the semi-arid environment of the central Flinders Ranges in South Australia. It describes the entire assemblage at order level and examines in more detail the differences in ant assemblages among habitats at both species and functional group level. The relative strength of the differences at species, functional group and order level are also compared. The correlation of patterns within the ant community with more subtle differences within a habitat resulting from ecological change due to grazing, fire and *Callitris* woodland regeneration, was also measured and compared at species, genus and functional group levels.

This chapter aims to answer two key questions. Firstly, how do arthropod assemblages vary among habitat types in this semi-arid environment? This is assessed at three contrasting levels; all arthropods at ordinal level, ants at species level, and ants at functional group level. Secondly, how do ant assemblages vary among sites impacted by grazing, fire and woodland regeneration? This is assessed at the level of ant species, and for functional groups.

2.2 Methods

2.2.1 Study sites

The central Flinders Ranges present a variety of habitat types, created by a difference in rainfall between the ranges and the more arid plains (Schwerdtfeger and Curran 1996) and the complex surface geology and geomorphology (Lemon 1996; Brandle 2001). These include native grassland, spinifex grassland, mallee and *Callitris* woodland, and chenopod shrubland. In addition, there are several sites that have been altered by stresses such as over grazing or disturbance events like fire, and altered habitat structure associated with different age stands of regenerating woodland. Rainfall in this region can vary considerably over relatively short distances and between years. Generally, the annual rainfall is below 300 mm. Soils in the area are predominantly red-brown calcareous loams with small patches of more neutral, fertile soils (Swaby 1971).

The Flinders Ranges National Park (FRNP) is made up of a number of former pastoral leases that have experienced very high stocking rates and this has lead to extreme degradation in some areas. This, combined with current grazing by goats, rabbits and kangaroos, has prevented the regeneration of native plant communities and lead to the wide distribution and high abundance of weed species. The removal of sheep, the success of Rabbit Haemorrhagic Disease and warren destruction, and the control of goats through ground mustering and aerial shooting, has not alleviated the total grazing pressure as euro (*Macropus robustus*) and red kangaroo (*Macropus rufus*) numbers remain high (DePreu 2000). Both native grassland and mallee sites have been affected by grazing.

The grassland study site (31 ° 25′ 05″ S, 138 ° 42′ 07″ E) was situated in a large open area of native tussock grassland dominated by *Stipa* spp. (spear grass) and was heavily invaded by a variety of exotic grass and herb species including *Bromus* spp. (brome grass) and *Asphodelus fistulosus* (onion weed) (nomenclature follows Black (1978)). Two 50 x 50 m plots, separated by approximately 100 m, were sampled; one was located in a 50 x 50 m exclosure established in 1999 that fenced out kangaroos but allowed access to smaller grazers such as rabbits, and the other (control) remained unfenced and open to grazing by all vertebrate herbivores. The use of this existing exclosure allowed a preliminary examination of correlations between ant communities and grazing regimes over a much longer time period than would have otherwise been possible in the time available for this project. In each case, five pitfall traps were arranged with one trap in the centre of the plot and the other four placed at the corners of a 14 x 14 m square (Figure 2.1a). This arrangement differed from that used at other sites, as the layout of traps was constrained by the shape of the existing exclosure.

The mallee sites were dominated by *Eucalyptus socialis* and *E. brachicalyx* (Barker 1971). There were two sites, one within the Flinders Ranges National Park (31 ° 21′ 45″ S, 138 ° 46′ 24″ E) with little understorey cover, and another in a less heavily grazed site with native shrub understorey on the Bunkers Reserve (owned by the Yellow-footed Rock Wallaby Preservation Society) (31 ° 24′ 20″ S, 138 ° 46′ 47″ E) that was much further from a watering point. At each site 10 pitfall traps were arranged in 2 rows of 5 traps each separated from the next by 10 m, and the two lines were 25 m apart (Figure 2.1b).

Spinifex or hummock grassland is dominated by *Triodia iritans*. It is usually found in pure stands, with small numbers of annual plants between the clumps (Barker 1971). Fire can greatly impact plant survival and recruitment in semi-arid environments (Hodgkinson and Griffin 1982) and spinifex communities are particularly sensitive to fire (Haydon *et al.* 2000). Two sites were chosen for this study; one with small tussocks that was regenerating after a fire in 1996 resulting from a lightning strike (Burnt, 31° 25′ 57″ S, 138° 43′ 26″ E) and another that had escaped the recent fire, remaining unburnt for several decades and had large clumps of spinifex with much smaller gaps in between (Unburnt, 31° 25′ 25″ S, 138° 42′ 32″ E). Ten pitfall traps were installed at each site in two rows of 5 traps, as in the mallee sites.

The regeneration of the northern cypress pine (*Callitris glaucophylla*) communities in the Flinders Ranges is currently causing some concern among land managers as large areas of regenerating trees appear to be invading other habitat types, especially native grassland (Arkell *et al.* 1996). Large scale recruitment of *Callitris* pines appears to be linked with successive rainfall events (Adams 1999), reduced grazing pressure (Arkell *et al.* 1996) and absence of fires (Bowman *et al.* 1988; Bowman and Latz 1993). The current stands of young trees are likely to have germinated in the 1970s (Arkell *et al.* 1996). Groves of young, regenerating trees exist in dense monotypic stands with little understorey surrounding an older parent tree (Early regeneration). Other sites in the area contain older trees (Mid regeneration) with an open herbaceous understorey consisting mainly of annual weeds (*Carrichtera annua*, *Echium lycopsis*, and *Bromus rubens*). In lightly grazed areas the most mature trees remain (Late regeneration), and the community consists of widely spaced large trees with an understorey of shrubs, including *Dodonaca lobulata* (hop bush), *Senna artemisioides* and occasionally *Maireana* sp. (Barker 1971). It is likely that the differences in understorey plant diversity are related to differences in grazing intensity at the sites (Thompson and Eldridge 2005).

A site representing each of the three stages was selected for this study (Late (31° 25′ 12″ S, 138° 46′ 27″ E), Mid (31° 25′ 18″ S, 138° 46′ 17″ E) and Early (31° 23′ 43″ S, 138° 42′ 28″ E)). Pitfall traps were arranged as in the Mallee sites for the Early and Mid regeneration sites that had some level of ground cover or a dense tree canopy. However, as the mature *Callitris* site had only a few large trees separated by large expanses of open ground, traps were placed in the vicinity of understorey vegetation under 20 trees each at least 20 m from the next (Figure 2.1c).

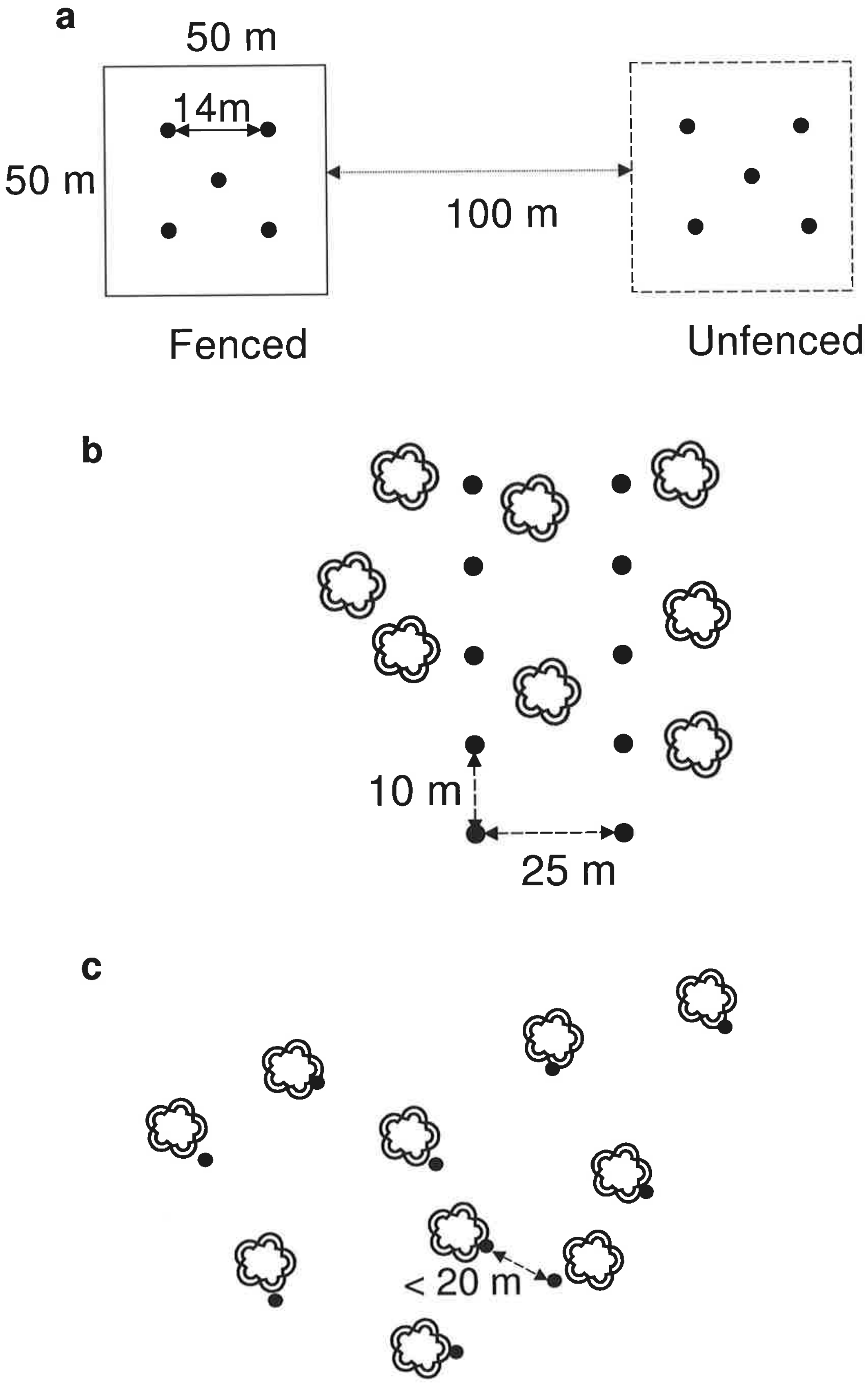


Figure 2.1 Layout of pitfall traps in **a)** Native grassland sites, **b)** Mallee woodland sites and **c)** Late regeneration *Callitris* woodland site. Black circles represent position of pitfall traps, other shapes represent trees. Not drawn to scale.

2.2.2 Experimental Design

Pitfall traps consisted of a 12 cm diameter round plastic food container, inserted inside a plastic flowerpot of slightly larger diameter and placed flush with the ground surface. The traps were half filled with saturated salt (NaCl) solution and 10-15 drops of detergent. All traps were opened on 26th October 2001, after being left closed for three weeks to lessen the 'digging-in effect' (Greenslade 1973), and were closed again five days later on 30th October. The traps were emptied every 24 h during this time.

At the end of the trapping period a 1 x 1 m grid of 10 cm squares was centred over each pitfall trap and 10 random grid points were chosen, excluding all points within 5 cm of the trap. A pen was placed at the chosen points and the height and type of vegetation (e.g. bare ground, litter, herb, grass) under the point was recorded. This information was used to test for correlations between arthropod abundances at various taxonomic levels and the characteristics of the vegetation within each plot.

2.2.3 Analysis

All arthropods caught in traps were identified to order level. Ants were further identified to genera using Shattuck (1999), separated to morphospecies, and assigned to functional groups according to Andersen (1995) (see Appendix 1 for a description of these functional groups). Non-metric Multidimensional Scaling (NMDS) (Sorensen's Distance measure) using PC-ORD 4.10 (McCune and Mefford 1999) was used to produce ordinations of arthropod community composition in individual pitfall traps at the sites. The ordination was constrained to two axes where possible, although three axes were needed at times to achieve a suitably low stress level. The variables in the three primary matrices were; a) abundance of arthropod orders; b) ant species abundance; and c) abundance of ant functional groups. Transformation of the data, including log (x+1) and range standardization where the abundance of each species or group is proportioned across all traps (Andersen and Majer 2004) (N. B. species with only single occurrences were not included in this method), were trialled to determine the ordination with the lowest stress value. For each of these ordinations, the correlation vectors ($r^2 > 0.2$) with environmental variables were plotted. Variables in the environmental (secondary) matrix were: site, plant height (average of all measurements), variance of plant height, and abundance of each ground cover category.

Multi-Response Permutation Procedures (MRPP), a non-parametric multivariate test for detecting significant differences between groups (McCune and Grace 2002), was used to test for the strength and significance of the separation of samples from the different habitats and among sites within a habitat type, under the different taxonomic groupings.

2.3 Results

2.3.1 Differences among habitat types

2.3.1.1 Patterns among epigaeic arthropod communities at order level

Twenty-six arthropod orders were collected from the four habitat types. The combined number of orders collected from all *Callitris* sites was the highest with 19 orders; however on an individual site basis the spinifex sites had the greatest number of orders (Table 2.1). The grassland sites had similar order level arthropod composition with relatively low numbers of ants and a relatively even spread across a number of orders including Collembola, Acarina, Hemiptera, Thysanoptera and other Hymenoptera, excluding ants (Figure 2.2). The spinifex sites were also similar to one another and to the native grassland sites, excepting that they contained larger proportions of Collembola.

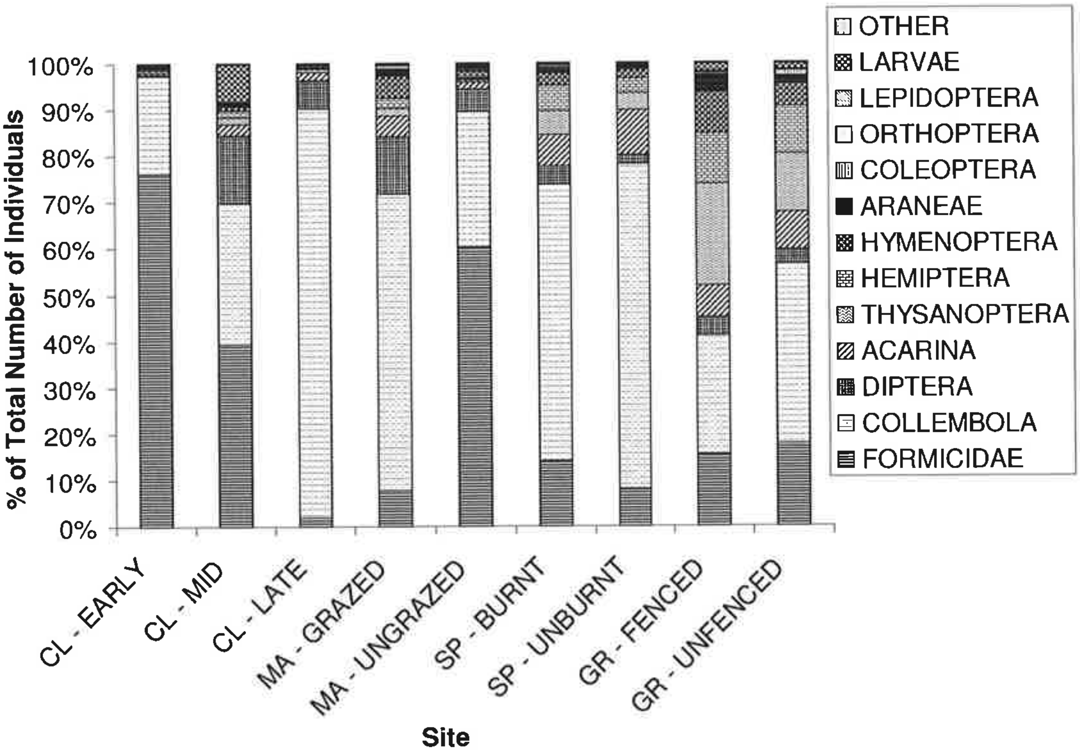


Figure 2.2 Epigaeic arthropod community composition at order level as measured by pitfall traps across sites with different habitat structure or cause of environmental change. CL – *Callitris* woodland, MA – Mallee woodland, SP – Spinifex and GR – Grassland.

The two woodland habitats (i.e. mallee and *Callitris* woodland) displayed a varied arthropod community among their sites. Ants made up a very large proportion of the community from the Early and Mid *Callitris* sites and the ungrazed mallee site, while Collembola made up the greatest proportion in the sites where ants were not so common. A large proportion of Diptera were also collected in traps in some of the woodland sites (Figure 2.2)

Table 2.1 Number of arthropod orders and ant species richness in pitfall traps at each site.

Site	Condition	Number of orders	Number of orders per trap	Number of ant species	Number of ant species per trap
Mallee	Grazed	10	1	43	4.3
	Ungrazed	9	0.9	35	3.5
	Total	14	0.7	53	2.7
Grassland	Fenced	9	1.8	18	3.6
	Control	9	1.8	13	2.6
	Total	15	1.5	23	2.3
Spinifex	Burnt	12	1.2	10	1
	Unburnt	12	1.2	14	1.4
	Total	16	0.8	20	1
Callitris	Early	9	0.9	30	3
	Mid	10	1	21	2.1
	Late	9	0.9	19	1.9
	Total	19	0.6	47	1.6

2.3.1.2 Patterns among ant communities

Ninety-nine ant species were found across the nine sites. The most common genera across all habitat types were *Iridomyrmex*, *Melophorus* and *Rhytidoponera*. *Camponotus* was collected in all habitats except the grassland sites. *Monomorium* and *Pheidole* were also widespread but were collected in relatively low numbers. Overall, the number of ant species collected in the mallee sites was higher than in any other habitat type and lowest in the spinifex grassland sites (Table 2.1). Two *Iridomyrmex* species were collected in the greatest numbers; *Iridomyrmex* sp. B (*rufoniger* group) with approximately 25,000 individuals collected and *Iridomyrmex greensladei* with an order of magnitude less at just under 2,500 individuals. Over 600 *Crematogaster frivola* were collected and more than 100 *Iridomyrmex* sp. C (*rufoniger* group), *Monomorium* sp. A (*rothsteini* group) and *Pheidole* sp. B. The next most abundant was *Rhytidoponera metallica,* while most other species were represented by less than 20 individuals.

Of the nine functional groups collected, Dominant Dolichoderines were extremely abundant in the *Callitris* woodland, native grassland and ungrazed mallee woodland sites. In contrast, Generalised Myrmicines were the most common group in the spinifex sites (Figure 2.3).

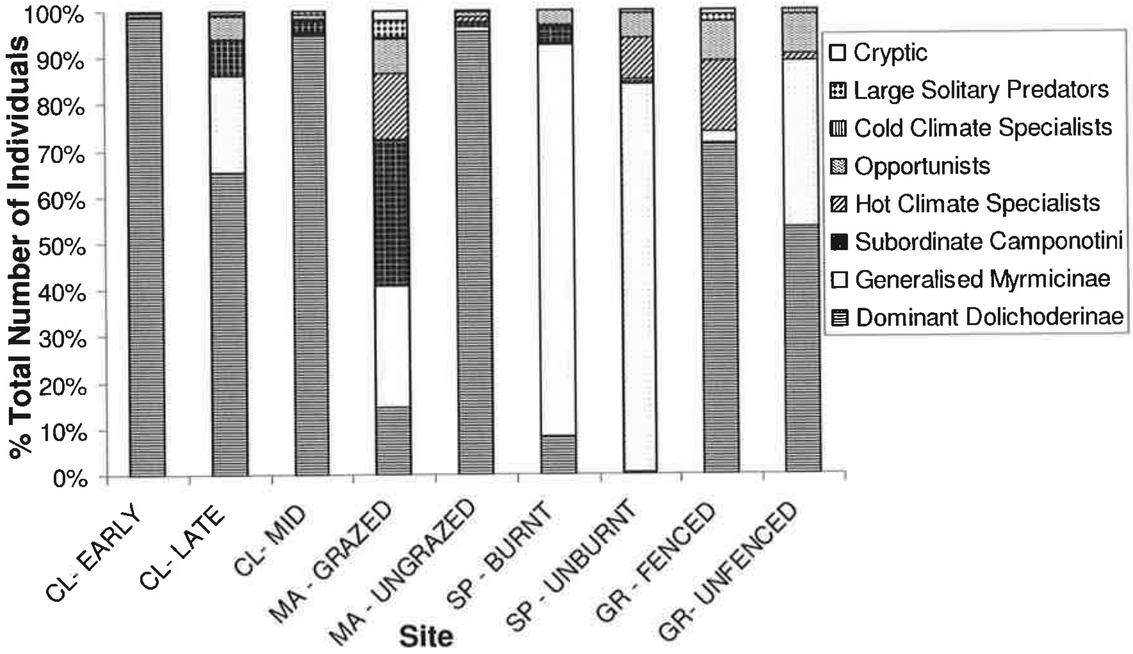


Figure 2.3 Functional group composition of ants collected in pitfall traps across sites with different habitat structure or cause of environmental change. CL – *Callitris* woodland, MA – Mallee woodland, SP – Spinifex and GR – Grassland.

2.3.1.3 Comparison of patterns among orders, ant species and ant functional groups

At order, species and functional group level NMDS ordination revealed a similar grouping of sites by habitat type except for the Early regeneration *Callitris* woodland, which tended to separate from the other two *Callitris* sites (Figures 2.4-6). While this pattern was evident at all three levels, the differences between the communities within the habitat types were greatest at ant species level (Table 2.2). In addition to the grouping by habitat type, the mallee and *Callitris* woodland sites grouped together and the native and spinifex grassland were similar to one another at all three taxonomic levels.

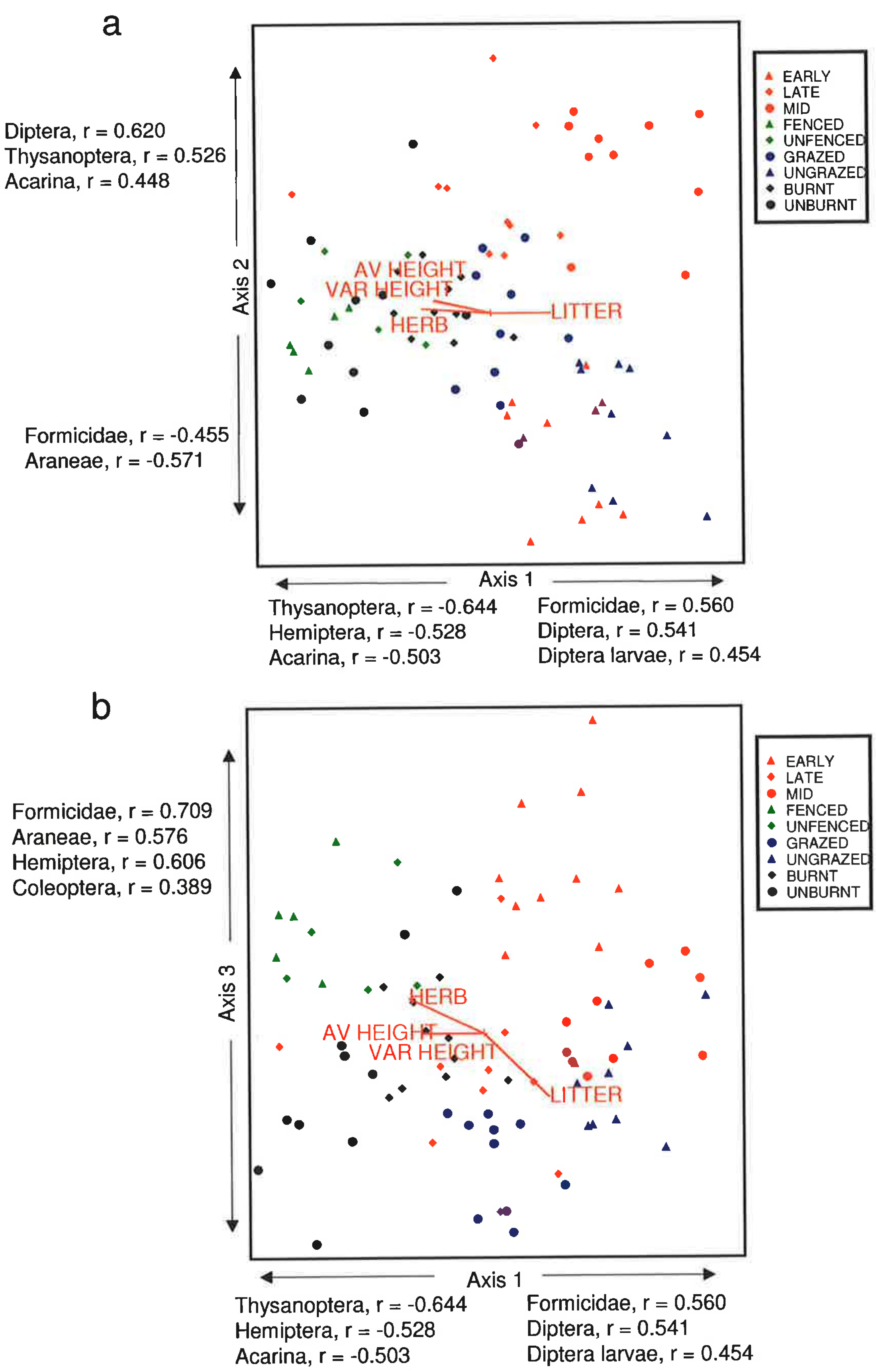


Figure 2.4 Three dimensional NMDS Ordination of all sites log (χ + 1) orders, (stress = 14.4, instability = 0.00007), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

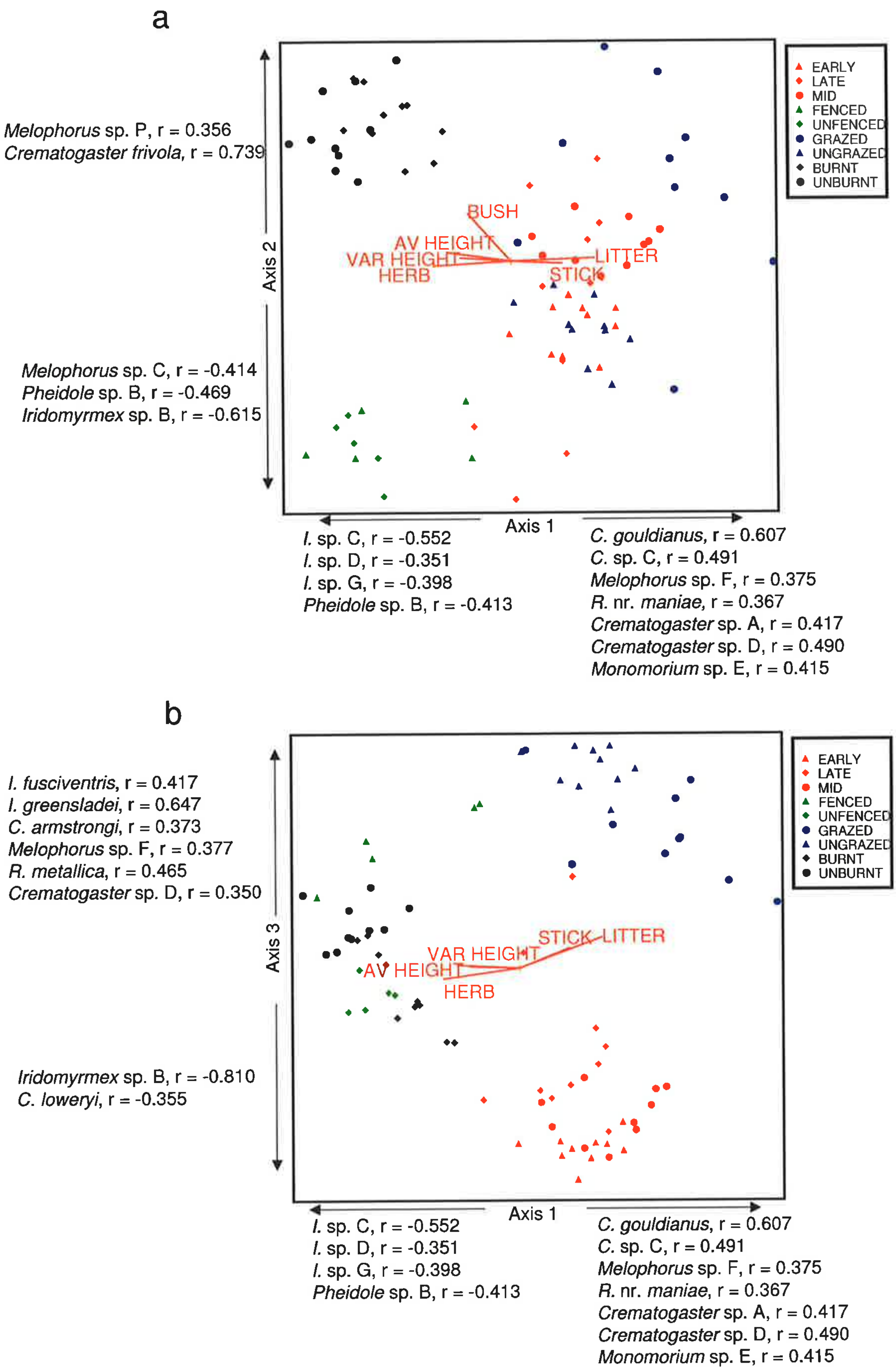


Figure 2.5 Three dimensional NMDS Ordination of all sites log (X+1) ant species, (stress 14.8, instability = 0.00007), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

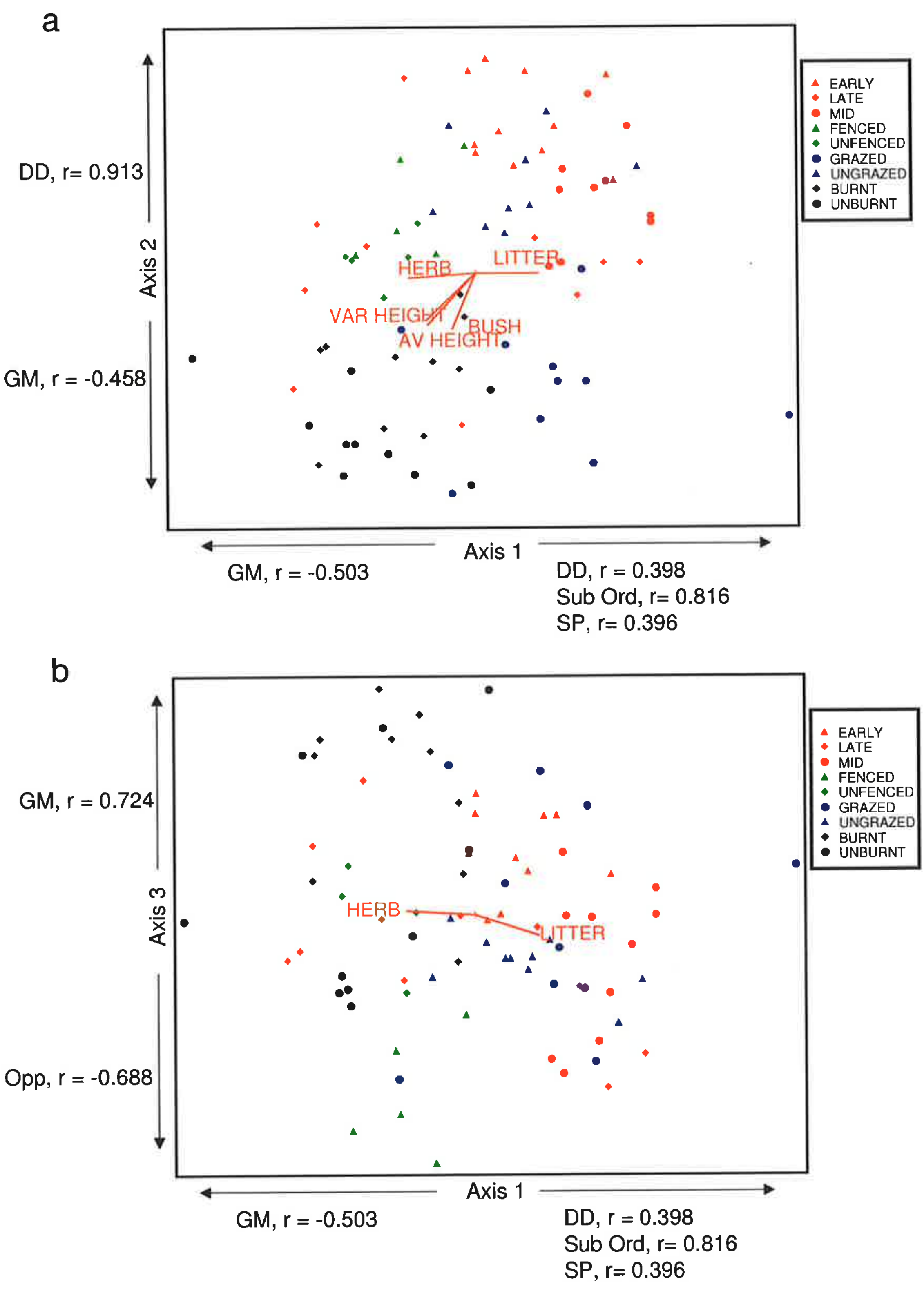


Figure 2.6 Three dimensional NMDS Ordination of all sites log (x + 1) ant functional groups (stress = 13.2, instability = 0.00010) **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, Sub Ord = Subordinate Camponotini, SP = Specialist Predators, Opp = Opportunists.

Table 2.2 Significance of groupings by habitat and site based on Multi-Response Permutation Procedures. *Greatest separation of groups (most negative T value), ◊Greatest within group homogeneity (highest A value).

Site	Taxa	Group	T	A	p
All	Orders	Habitat type	-16.983	0.163	<0.001
	Orders (log x+1)	Habitat type	-38.103	0.378	<0.001
	Common Orders (log x+1)	Habitat type	-38.014	0.403	<0.001
	Ant Functional Group	Habitat type	-17.693	0.169	<0.001
	Ant Functional Group (log x+1)	Habitat type	-35.132	0.435	<0.001
	Ant Species	Habitat type	-31.484	0.219	<0.001
	Ant Species (range standardised) ◊	Habitat type	-36.25	0.473	<0.001
	Ant Species (log x+1)*	Habitat type	-39.938	0.387	<0.001
Spinifex	Order (log x+1)	Site	-3.691	0.051	0.002
	Ant Functional Group ◊	Site	-4.076	0.125	0.007
	Ant Species (range standardised)	Site	-2.77	0.052	0.017
	Ant Species (log x+1)*	Site	-4.841	0.105	0.002
Callitris	Order (log x+1) ◊*	Site	-14.52	0.311	<0.001
	Ant Functional Group (log x+1)	Site	-11.326	0.265	<0.001
	Ant Species (range standardised)	Site	-10.347	0.085	<0.001
	Ant Species (log x+1)	Site	-12.745	0.187	<0.001

Table 2.2 cont.

Site	Taxa	Group	T	A	p
Grassland	Order (log x+1)	Site	-1.302	0.040	0.104
	Ant Functional Group (log x+1) ◊	Site	-4.153	0.228	0.003
	Ant Species (range standardised)	Site	-4.022	0.143	0.001
	Ant Species*	Site	-4.756	0.150	0.001
Mallee	Order (log x+1)	Site	-9.235	0.157	<0.001
	Ant Functional Group*◊	Site	-10.664	0.265	<0.001
	Ant Functional Group (log x+1)	Site	-9.669	0.208	<0.001
	Ant Species (range standardised)	Site	-0.875	0.007	0.187
	Ant Species	Site	-10.561	0.186	<0.001
	Ant Species (log x+1)	Site	-9.386	0.121	<0.001

Correlations of habitat variables with the two broad groups of woodland and grassland sites, and the various orders, species and functional groups that differentiated them, were also similar in all ordinations. These included a greater cover of litter in the woodland sites and a greater height of vegetation, variation in vegetation height and cover of herbs with the grasslands. However, the position of the *Callitris* sites in the ordination was influenced by large numbers of *Iridomyrmex* sp. B in the ant community but this did not correlate with any of the environmental variables measured (Figure 2.5 a, b)

2.3.2 Variation within habitat types

2.3.2.1 Spinifex grassland

The two spinifex sites displayed very similar ordinal arthropod community compositions (Figure 2.2) and, not surprisingly, there was no obvious separation of the two sites in the ordination (Figure 2.7). Some correlation with environmental variables at the trap level was evident, with Thysanura and Araneae correlating with greater cover of herbs and litter, and Coleoptera with more bare ground, spinifex and variation in height of vegetation. The abundance of Hymenoptera and Diptera also correlated with the cover of grass.

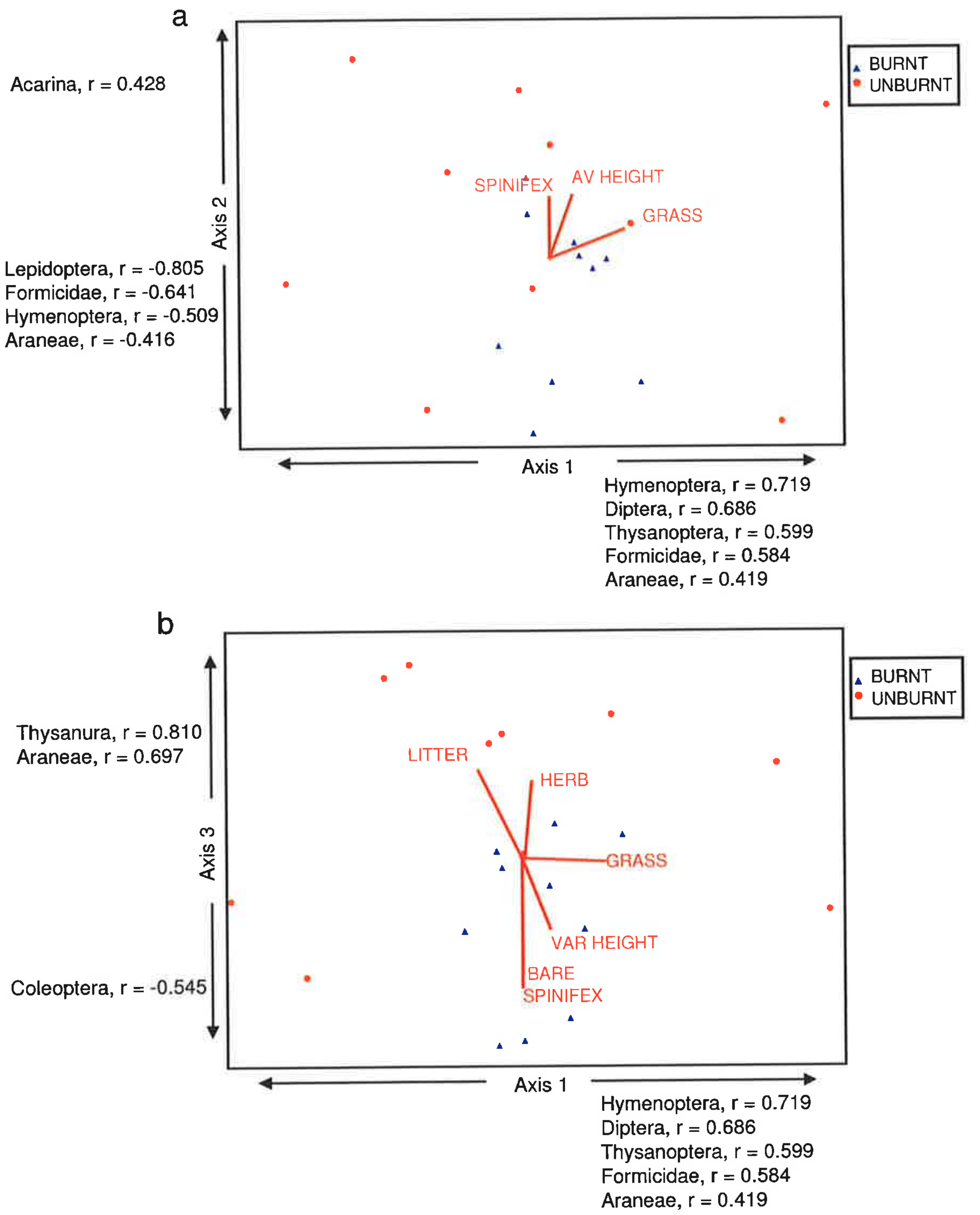


Figure 2.7 Three dimensional NMDS Ordination of spinifex log orders (stress = 12.77, instability = 0.0049), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

Ant species richness was slightly higher at the unburnt spinifex site (14 species) than at the burnt site (10 species) (Table 2.1). When the ant community structure was compared, there appeared to be some level of separation of the burnt and unburnt sites (Figure 2.8). The burnt sites correlated with more bare ground and unburnt with more litter. The different positions were largely due to greater numbers of *Iridomyrmex* sp. B, *C. cinereus amperi* and *C. frivola* in the burnt sites and higher abundances of two *Melophorus* species and *R. metallica* in the unburnt sites. This split was also partly evident at functional group level and the correlated environmental variables were similar (Figure 2.9). The functional groups that explained the position of the traps along the same axis to a large degree were Dominant Dolichoderinae, Subordinate Camponotini and Generalised Myrmicinae, which encompass the species most relevant to the position of the burnt site mentioned above.

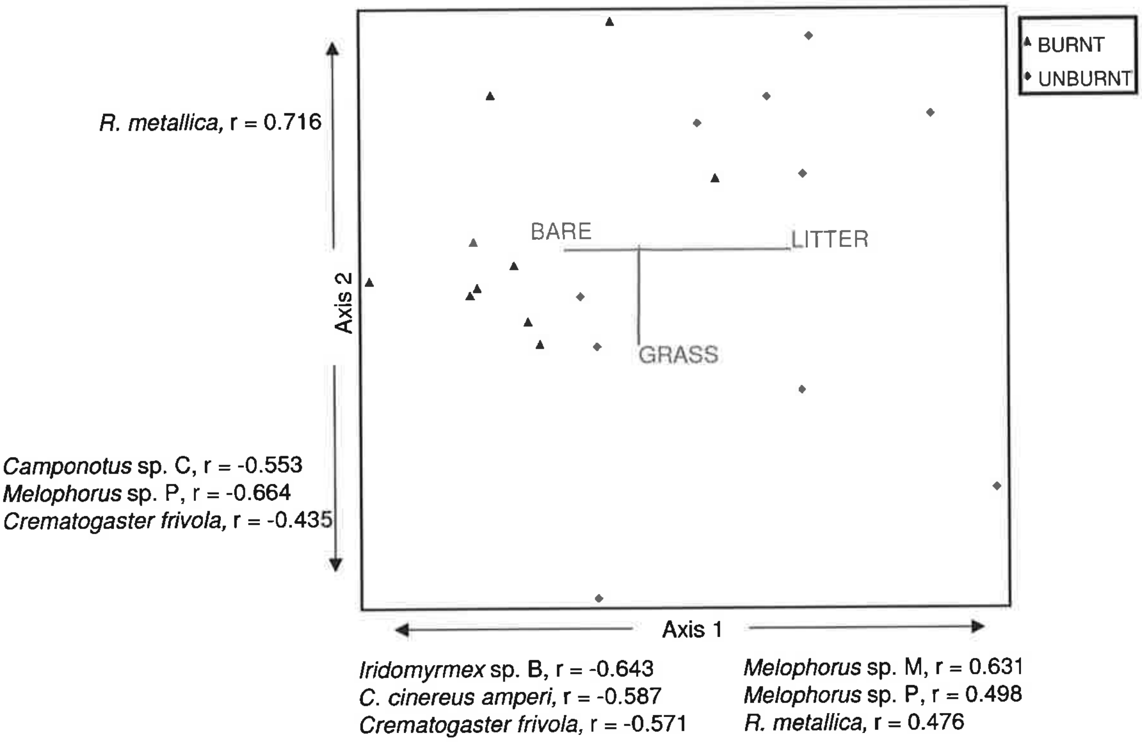


Figure 2.8 Two dimensional NMDS Ordination of spinifex log ant species (stress = 12.5, instability = 0.00008). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

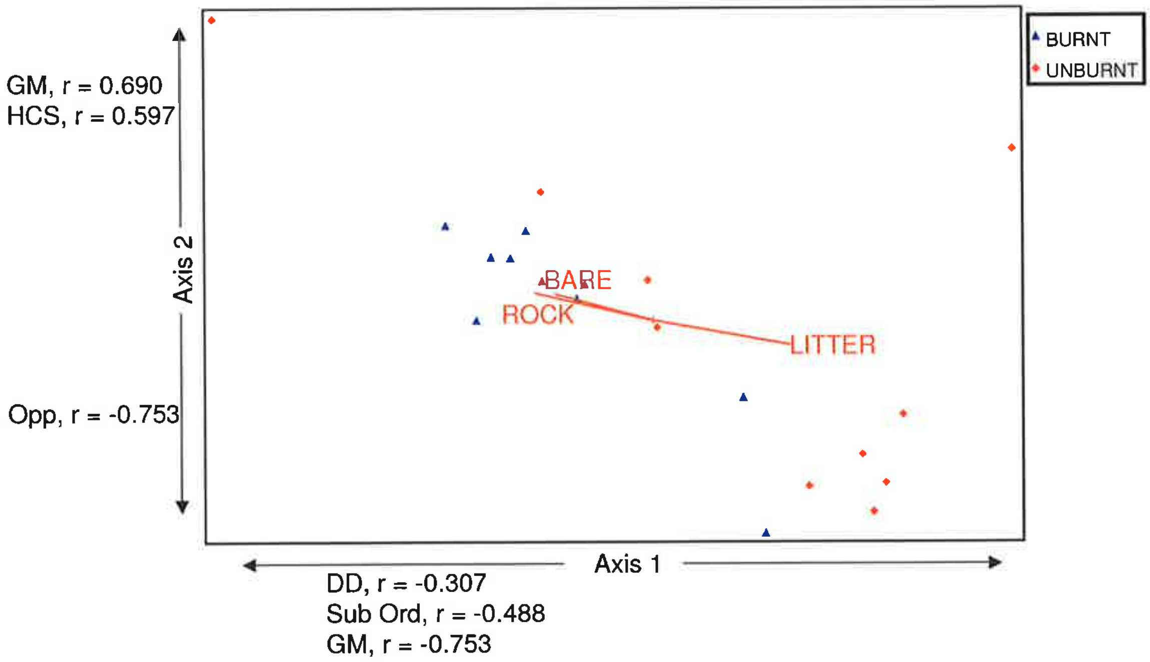


Figure 2.9 Two dimensional NMDS Ordination of spinifex ant functional groups (stress = 5.7, instability = 0.0001). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, Sub Ord = Subordinate Camponotini, SP = Specialist Predators, Opp = Opportunists, HCS = Hot Climate Specialists.

The log morphospecies data provided the best separation of sites while the within site homogeneity was greatest at the level of ant functional groups (Table 2.2).

2.3.2.2 *Callitris* woodland

The arthropod community varied considerably across the three *Callitris* woodland sites (Figure 2.2). The Early regeneration site was dominated by a high abundance of ants and Collembola, and the Mid site by fewer ants, some Collembola and large numbers of Diptera. In contrast, far fewer ants were found in the Late regeneration site but large numbers Collembola were collected. The ordination of the arthropod community structure reflected these large differences in composition (Figure 2.10). The position of the Early regeneration site was largely explained by the larger numbers of ants, spiders and Hemiptera, and correlated with more bare ground and rocks. The Mid and Late site positions were explained by fewer ants and more Thysanoptera and Diptera, and correlated with a greater average height of vegetation. The Mid site in particular was linked to greater numbers of Diptera and correlated with more litter cover on the ground.

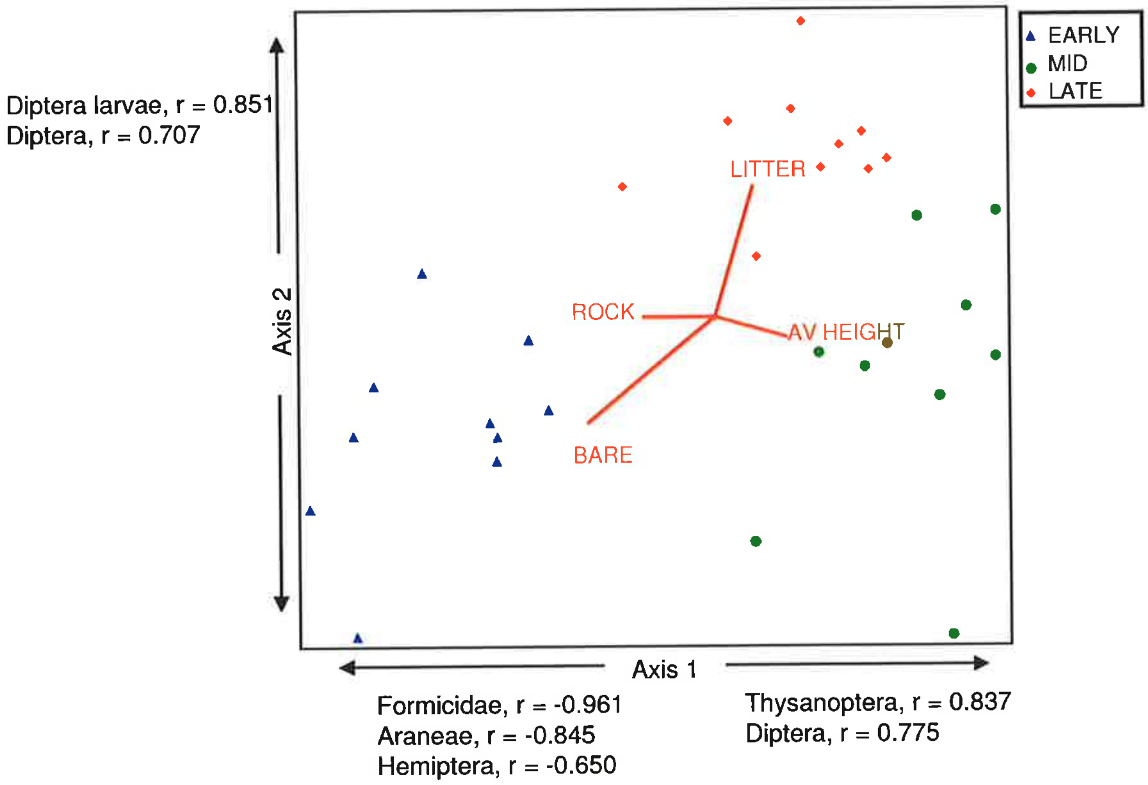


Figure 2.10 Two dimensional NMDS Ordination of *Callitris* woodland log orders (stress =12.86, instability = 0.00002). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

At the ant community level, differences were also apparent between the three sites. Ant species richness decreased from the Early site with 30 species through to the Late stage regeneration site with 19 species (Table 2.1). A gradation in community composition of the sites was also evident with the Early site being correlated with more bare ground, the Late site with more sticks, height and structural diversity, and the Mid site being positioned between these two (Figure 2.11). The position of the Early site traps correlated with greater numbers of *Iridomyrmex* sp. B and G, *C. consobrinus*, *Melophorus* sp. C and H and *Monomorium* sp. A. The Late site trap positions were largely due to more *I. greensladei*, *Pheidole* sp. B, *R. metallica*, and *Crematogaster* sp. A.

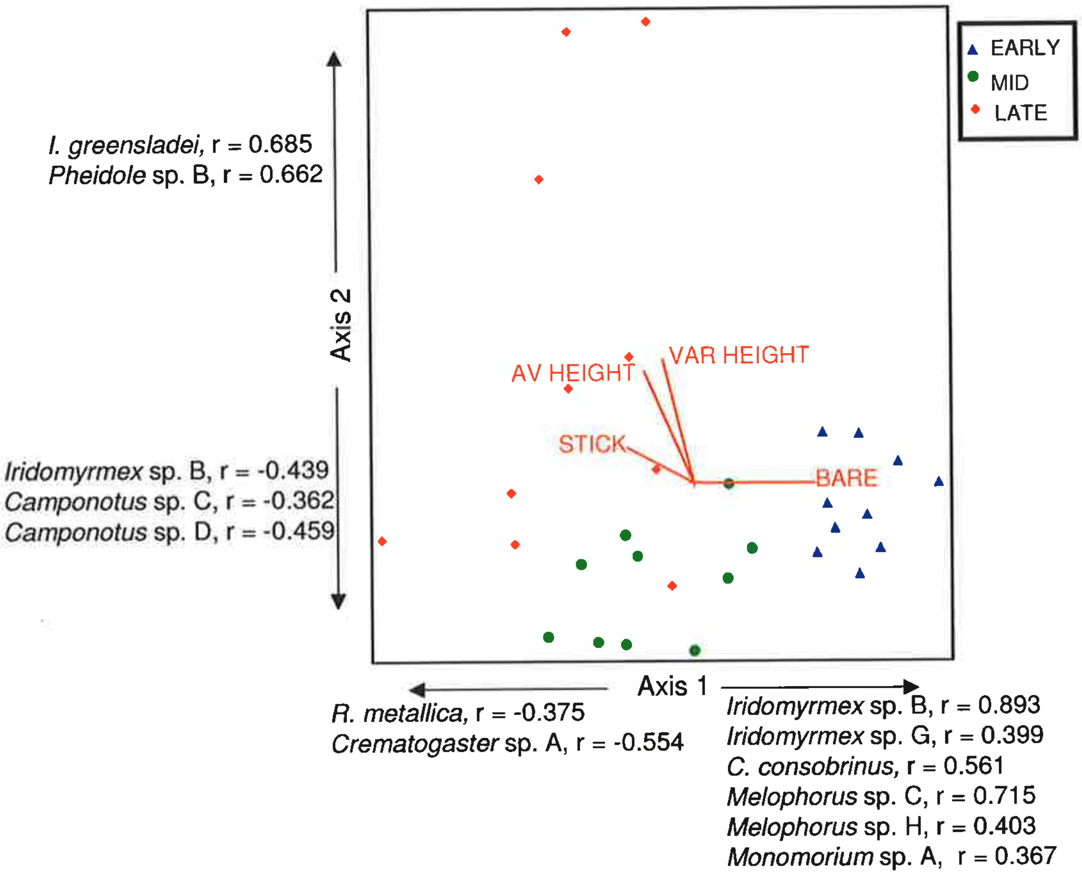


Figure 2.11 Two dimensional NMDS Ordination of *Callitris* woodland log ant species (stress =14.2, instability = 0.00000). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

The pattern produced at the ant functional group level (Figure 2.12) is similar to that for species. The functional groups that were most influential in separating the sites were Dominant Dolichoderinae and Hot Climate Specialists for the Early site, which correlated with more bare ground, and Sub-Ordinate Camponotini, Opportunists and Solitary Predators for the Mid stage regeneration site, which correlated with more litter. Of the three taxonomic groupings, log (x+1) orders provided the strongest separation of the three sites and the most homogeneous communities within each site (Table 2.2).

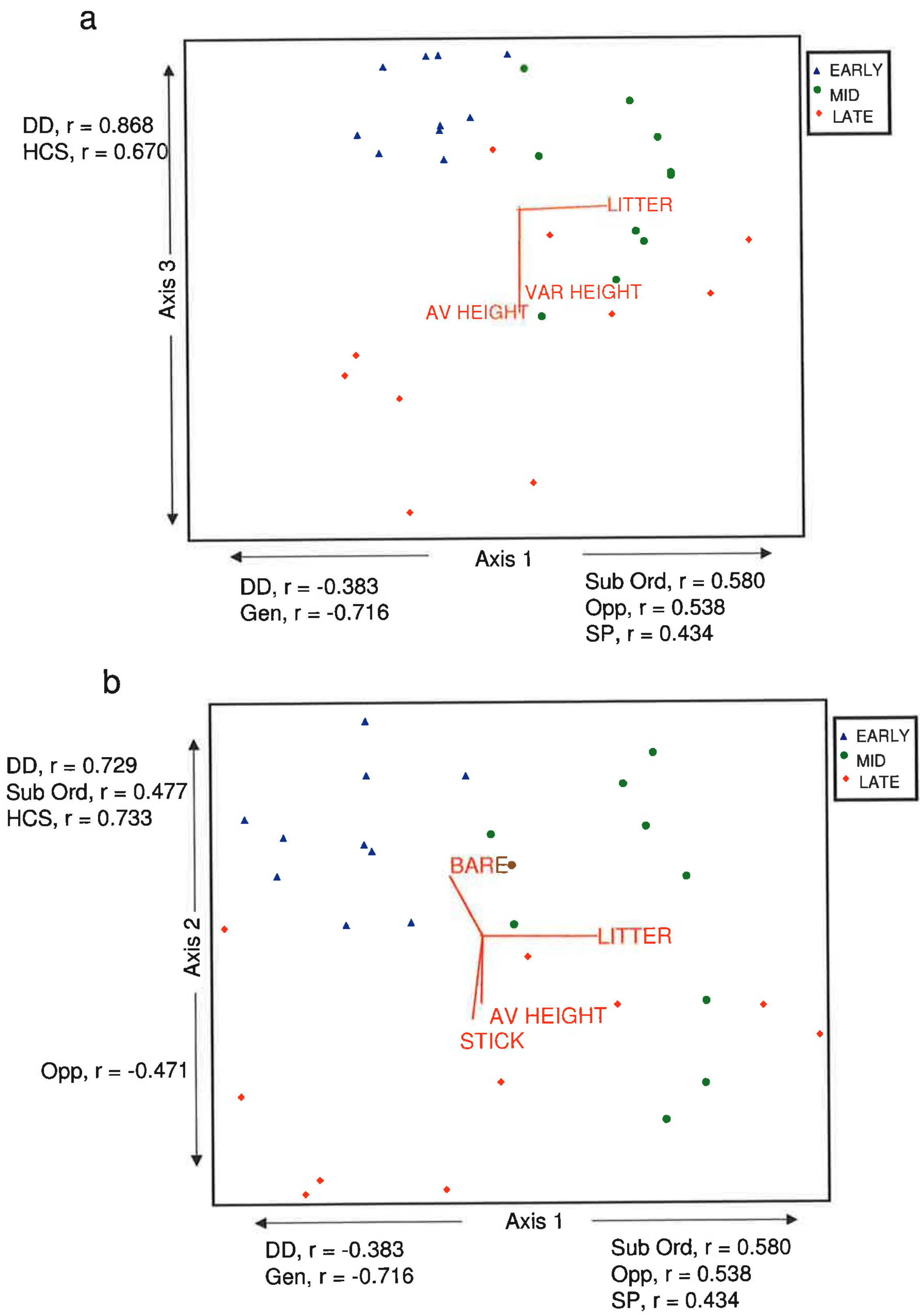


Figure 2.12 Three dimensional NMDS Ordination of *Callitris* log ant functional groups, (stress = 9.4, instability = 0.00009) **a)** Axes 1 and 3 and **b)** Axes 1 and 2. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, Sub Ord = Subordinate Camponotini, SP = Specialist Predators, Opp = Opportunists, HCS = Hot Climate Specialists.

2.3.2.3 Native grassland

The order level arthropod communities of the two grassland sites were very similar and were made up predominantly of ants, Collembola, Acarina, Thysanoptera and Hemiptera (Figure 2.2). Although the separation of the two sites on the ordination was not significant, the community composition of the two sites differed to some degree with the fenced site having a greater abundance of grass and greater variation in height of vegetation, which correlated with a greater abundance of spiders, Lepidoptera, Coleoptera and Thysanoptera (Figure 2.13).

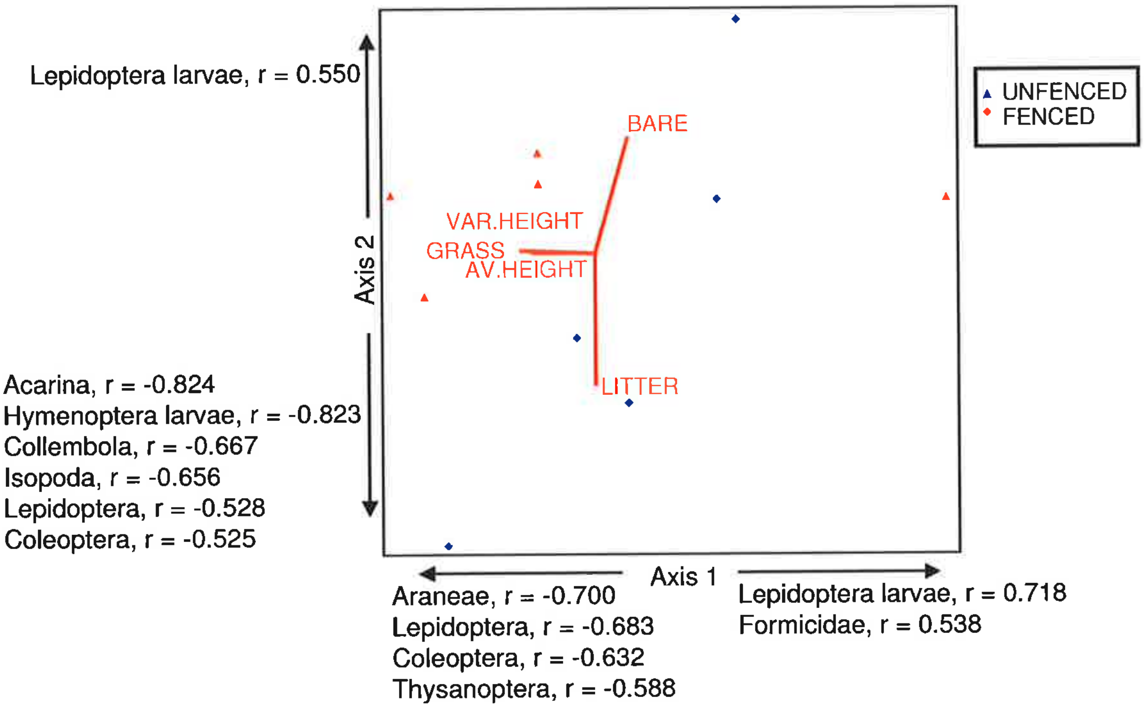


Figure 2.13 Two dimensional NMDS Ordination of grassland log orders (stress = 9.202, instability = 0.0008). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

Ant species richness was relatively low in both native grassland sites. The unfenced plot contained only 13 species; while 18 species were collected in the fenced area (Table 2.1). The community composition was different between the two sites with a number of small *Iridomyrmex* spp. and *R. metallica* being well represented in the unfenced site and this correlated with more grass cover and greater variation in height. The large *I. greensladei* and a small number of *Melophorus* spp. explained the position of the fenced site and correlated with more herbs and litter in the habitat (Figure 2.14).

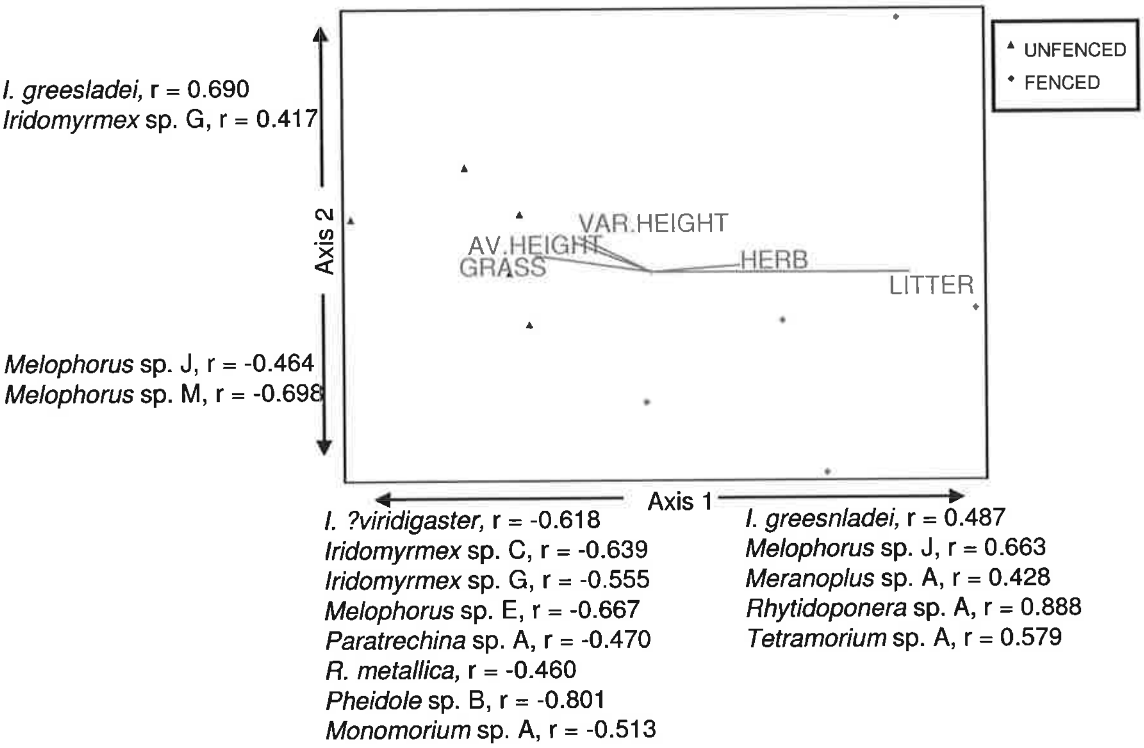


Figure 2.14 Two dimensional NMDS Ordination of grassland ant species (stress = 6.579, instability = 0.0009). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

The pattern produced by the functional group composition was similar to that at species level (Figure 2.15). The most important groups were the Generalised Myrmicinae and Hot Climate Specialists in the fenced site and these correlated with more litter, and the Cold Climate Specialists and Dominant Dolichoderinae in the unfenced site, which correlated with more grass and greater average height of vegetation. The separation of the sites by ant morphospecies was the strongest, while log functional groups provided the greatest within site homogeneity (Table 2.2).

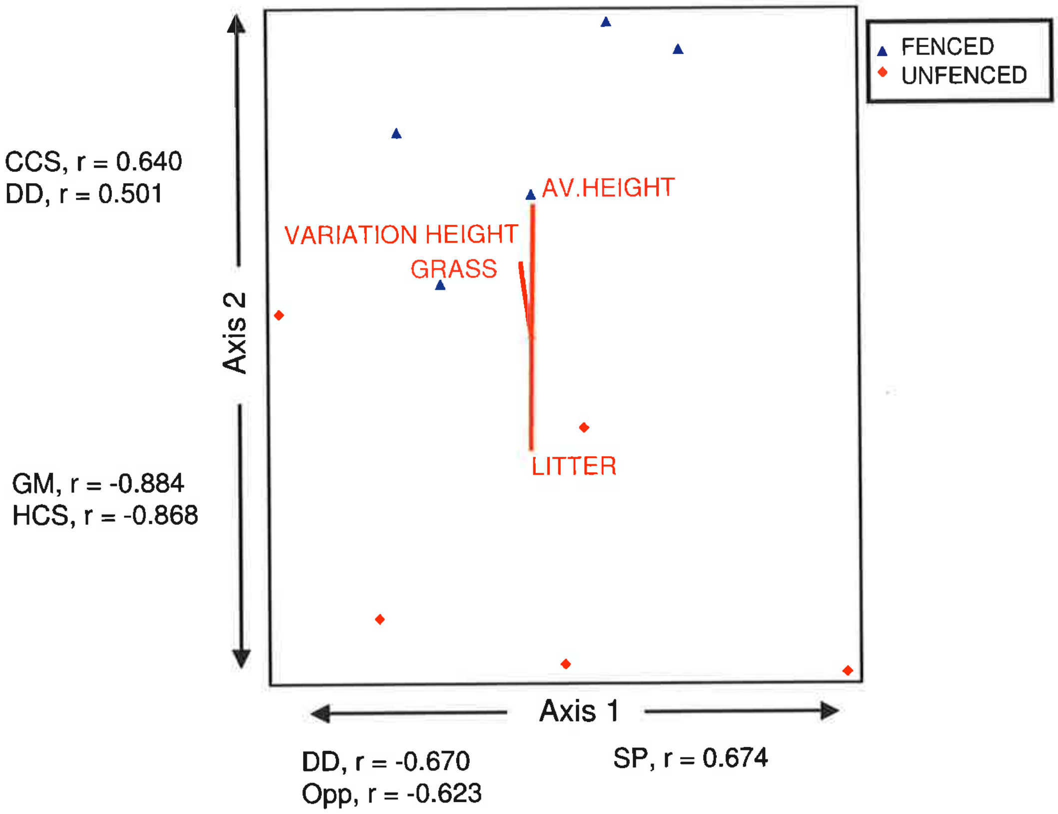


Figure 2.15 Two dimensional NMDS Ordination of grassland log ant functional group, (stress = 9.29, instability = 0.0047). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, CCS = Cold Climate Specialists, SP = Specialist Predators, Opp = Opportunists, HCS = Hot Climate Specialists.

2.3.2.4 Mallee woodland

The ungrazed mallee site was characterised by a much larger proportion of ants, while the grazed site had higher proportions of Collembola and Diptera (Figure 2.2). These two orders plus a larger proportion of Thysanoptera and Hemiptera explained the separation of the two sites, but no environmental variables correlated with these differences (Figure 2.16).

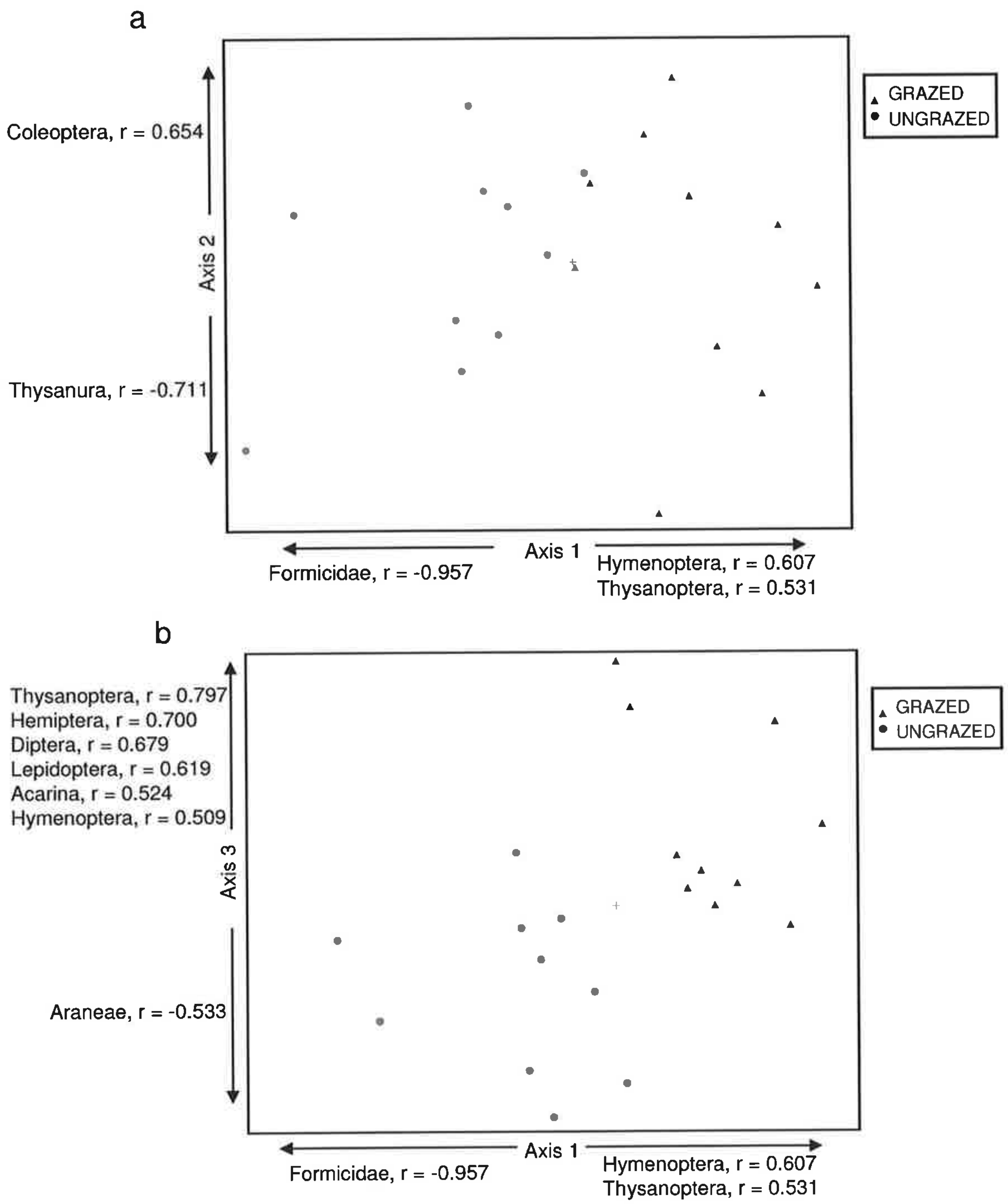


Figure 2.16 Three dimensional NMDS Ordination of mallee log orders (stress = 13.4, instability = 0.0047), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

Ant species richness of these two sites was much higher than the other habitats with 43 species collected in the grazed Mallee site and 35 species in the ungrazed site (Table 2.1). The two sites also separated on the basis of their ant species composition (Figure 2.17). A number of species contributed to the separation but the large numbers of *I. greensladei* collected in the ungrazed Mallee site was the most obvious. Once again, there was no correlation with any environmental variables.

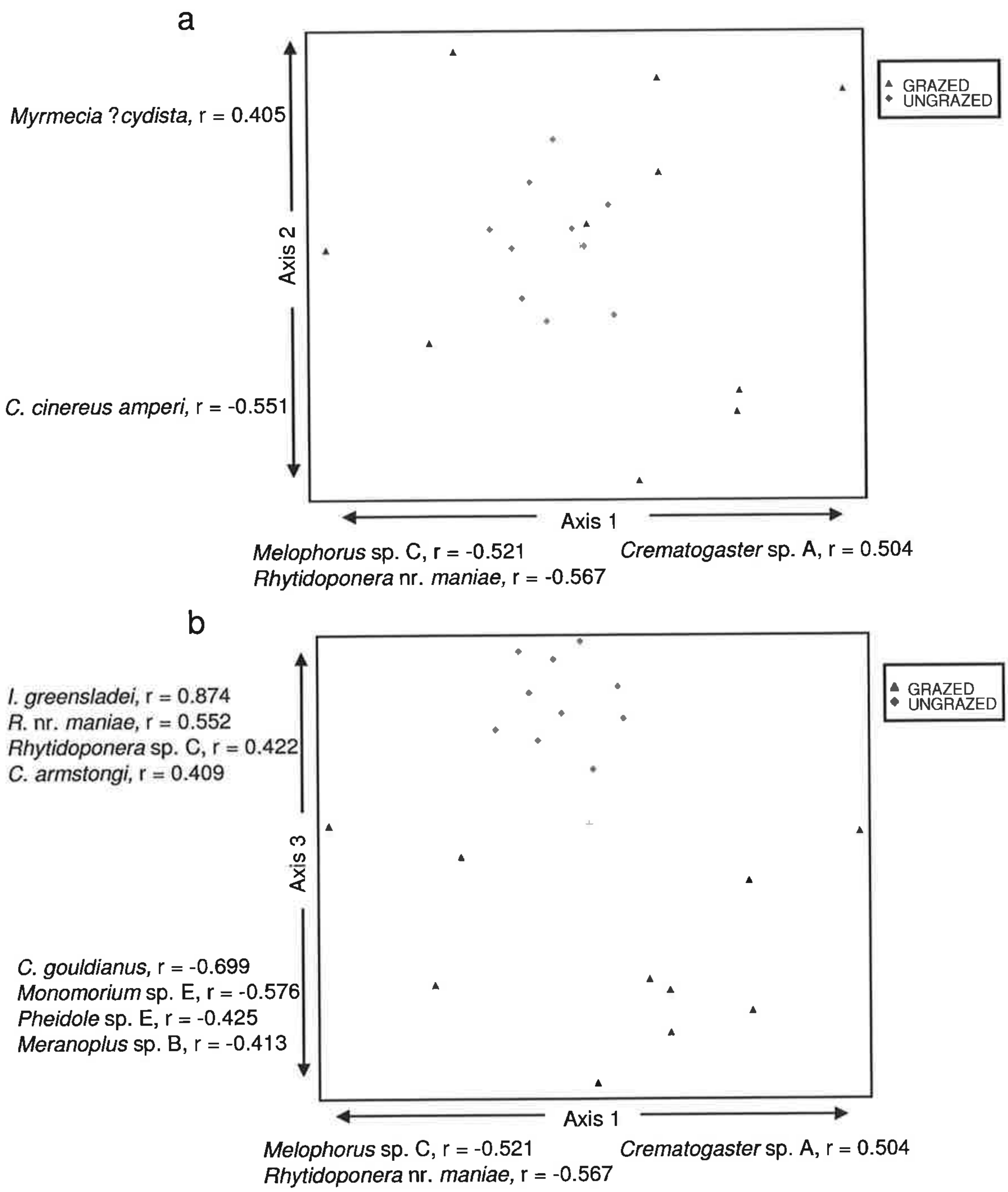


Figure 2.17 Three dimensional NMDS Ordination of mallee log ant species (stress = 12.68, instability = 0.00369) **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$).

The Dominant Dolichoderinae were the most influential functional group producing a similar difference between the ant communities at this level, but there was no correlation with any environmental variables (Figure 2.18). Functional groups gave the best separation of the sites and greatest within site homogeneity for the Mallee sites (Table 2.2).

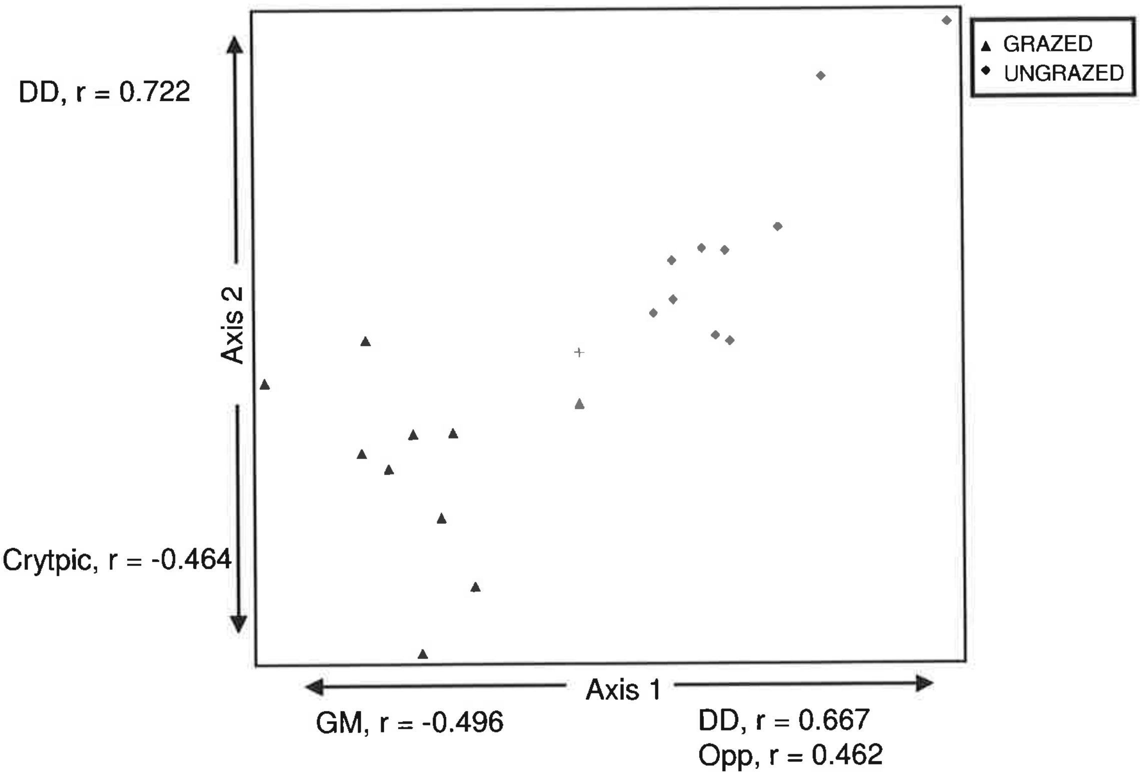


Figure 2.18 Two dimensional NMDS Ordination of mallee ant functional groups (stress = 8.69, instability = 0.003). Samples from each site have a unique symbol and the correlations with environmental variables are shown as vectors ($r^2 \geq 0.2$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, Opp = Opportunists, Cryptic = Cryptic Species.

2.4 Discussion

The arthropod and ant communities across the nine surveyed sites displayed similar patterns, with the clearest differences between habitats and sites influenced by grazing, fire and woodland regeneration being at the level of ant species, in all but the *Callitris* woodland habitat. Ant species level is also more likely to provide information of use in teasing apart the most important variables associated with ecological variation in these environments. However, among the *Callitris* sites the greatest differences were found at order level.

The two woodland and the two grassland habitats showed similarities at both the order and ant community levels. The woodland and grassland habitats each had habitat structural attributes in common and variables, such as the amount of variation in height of vegetation, were linked with arthropod and ant community composition. This suggests that the physical structure of vegetation influences the composition of the arthropod community in this system, as has been shown in other environments (e.g. Morris 2000). Another, and not mutually exclusive, explanation is the provision of a common food resource, the availability of which is not greatly affected by the history of environmental stress or disturbance within each habitat type. The grassland habitats are likely to provide a source of seeds, and they support a greater proportion of Generalised Myrmicine ants and seed harvesting *Pheidole* spp. (Briese 1982a; Shattuck 1999; Cooke 2003). The trees and understorey shrubs in the woodland sites may also provide a source of liquid carbohydrates through either extrafloral nectaries or insect honeydew. Such resources are particularly important for Dominant Dolichoderines (Greenslade 1971; Andersen 2003), and this may account for their greater proportional abundance in the woodland sites.

Useful comparisons can be made between the ant assemblages found in each habitat type and those from a survey conducted 30 years previously in similar locations and habitats around Oraparinna and at a similar time of year (Greenslade 1971). The total number of species collected, as well as the number collected in each habitat type, is comparable to the current study, despite the use of a wider range of collecting techniques in the earlier survey. A total of 51 ant species were collected in the mallee habitats in the earlier study compared with 53 here. The *Callitris* woodland areas had 36 species and the grassland sites, including spinifex grassland, were again the least diverse habitats with 21 species. The ant community composition within each habitat type at the level of genus is also comparable, with similar genera represented in each habitat type. The most common and widespread genera, such as *Iridomyrmex*, *Pheidole*, *Monomorium* and *Rhytidoponera*, had a similar distribution across the habitats in both studies.

The structure of ant communities varied both between and within habitat types in the current study, especially at species level. The greatest differences appear to be due to the relative abundance of the dominant ant species, *Iridomyrmex* sp. B. This species was collected in exceptionally high numbers in the *Callitris* woodland site that contained dense stands of young trees, but not the other two *Callitris* sites. It was also found in higher numbers in the burnt spinifex site than the unburnt site, in contrast to greater numbers of a less competitive opportunist, *R. metallica*, in the unburnt site. There was a correlation between the abundance of this *Iridomyrmex* species and the amount of bare ground in the habitat. *Iridomyrmex* species tend to predominate in warm open environments (Andersen 2003) but it is difficult to speculate on the causes of these ant community differences because of the lack of replication in this survey.

Of the three levels compared in this study (order, ant functional group, and ant morphospecies) morphospecies data, when log transformed, generally gave the best separation on the basis of habitat type and between sites within a habitat. However, functional groups also produced good separation of the sites, especially in the diverse mallee habitat. This level has a number of features in its favour including the fact that sorting to functional groups is much more time efficient than to species level. At functional group level, the variation related to high species richness and species turnover between traps associated with the distribution of nests is also reduced, resulting in much more homogenous community composition within sites. Correlations between ant community structure and habitat variables were also evident for functional groups, suggesting that these groups may be a relevant and meaningful concept in terms of ecosystem processes (Chapin *et al.* 1992).

In conclusion, the results of this study suggest that comparing patterns within ant communities can be useful for discerning differences between sites within the semi-arid habitats of the Flinders Ranges, predominantly at species level but also for functional groups. These patterns reflect differences among the ordinal epigaeic arthropod communities, and correlate strongly with a range of environmental variables.

CHAPTER 3: THE IMPACT OF PERENNIAL SHRUB LOSS ON ARTHROPOD DIVERSITY AND COMMUNITY STRUCTURE IN CHENOPOD SHRUBLAND, WITH SPECIAL REFERENCE TO ANTS

3.1 Introduction

As plants are sessile, the effect of stress or disturbance on vegetation is relatively easy to measure. If patterns within the plant community reflected changes within other less easily measured parts of the community or ecosystem this would make them ideal indicators of the broader impacts of ecological change (Pearson 1996; Landsberg and Crowley 2004).

Plant species richness has been shown to be positively correlated with the species richness of arthropods in grasslands (Siemann *et al.* 1998), lizards and scorpions in semi-arid woodland (Abensperg-Traun *et al.* 1997), grasshopper (Ludwig *et al.* 2004) and butterfly diversity (Arnold *et al.* 1999) in semi-arid shrubland, Homoptera in old fields (Murdoch *et al.* 1972) and ant species richness during minesite rehabilitation (Majer *et al.* 1984). Positive relationships have also been found between vegetation structural diversity and the diversity of a variety of taxa from birds (MacArthur and MacArthur 1961; Whitford *et al.* 1998) to lizards (Pianka 1967) to arthropods (Lawton and Schroder 1977; Morris 2000), from groups as diverse as arthropods (Lawton and Schroder 1977; Morris 2000) to individual orders (Murdoch *et al.* 1972; Abensperg-Traun *et al.* 1997), and from a wide range of climates and habitat types (MacArthur and MacArthur 1961; Abensperg-Traun *et al.* 1997; Whitford *et al.* 1998; Morris 2000).

While not all studies have noted a change in species richness as a result of changes within the vegetation (e.g. Kremen 1992), many other studies have found significant impacts on community composition of various groups, including ground dwelling arthropods (e.g. Longcore 2003), spiders (e.g. Harris *et al.* 2003), beetles (e.g. Luff and Rushton 1989), grasshoppers (e.g. Andersen *et al.* 2001) and ants (e.g. Andersen *et al.* 2004). However, the evidence that patterns within plant communities universally reflect all other parts of the ecosystem or in all habitats is far from conclusive, and it has been suggested that the use of plant floristic or structural diversity as indicators of faunal groups should be validated in each environment and with each type of stress or disturbance history (Abensperg-Traun *et al.* 1996; Abensperg-Traun *et al.* 1997).

In semi-arid environments, as in any ecosystem, plants create physical structure, provide shade and shelter, and produce a variety of food resources for other organisms. They reflect the physical environment (Landsberg and Crowley 2004) and many aspects of ecosystem function (Ludwig *et al.* 2004). Environmental stresses such as high grazing pressure can have large impacts on the physical structure, community composition and function of arid shrublands, and the modifications within the plant community are often reflected in faunal communities (Majer and Beeston 1996; Read 2002; Ludwig *et al.* 2004)

Arthropods are likely to respond to variation within the plant communities of arid habitats. Alterations in plant species abundance and diversity are likely to affect species rich groups such as Hemiptera, Orthoptera, Lepidoptera, Coleoptera and Hymenoptera that are reliant on plant products for food, at least for part of their lifecycle. Other taxa, such as spiders, require structure provided by vegetation for shelter, shade and web support, and these and other predatory groups may be affected indirectly by the impact of vegetation change on their invertebrate food supply.

The aim of this chapter is to detect correlations between the structure of the arthropod community (at order level) and vegetation patterns, in particular, the presence or absence of shrubs. Particular attention was paid to the response of the ant community.

Ants are one of the most abundant and species-rich arthropod groups within semi-arid shrubland communities (Briese and Macauley 1977; Greenslade and Greenslade 1984b). Warm and open habitats provide the optimum conditions for a wide range of ant species, especially members of the behaviourally dominant genus *Iridomyrmex* (Andersen 2003). Changes within a habitat associated with soil, shade and litter are therefore likely to impact on ant communities (Andersen 2003). In more mesic and hence shadier habitats ants seek radiation from the sun (Andersen 1986, 1991). However, within warmer, drier environments where access to solar radiation is not limited, structure that provides shade may be sought by ants to keep cool. Alternatively, while shade and structure may be important in arid environments, other factors such as access to certain food resources may be of far greater consequence. Arid shrublands also provide ant species with important food resources including seeds, nectar and honeydew. The presence of honeydew in particular may directly control the productivity and community structure of ants in these environments (Greenslade 1971; Andersen 2003).

Assigning ants to functional groups can overcome the taxonomic difficulties and lack of knowledge associated with species level identifications, requiring only identification to the level of species-group or genus (Greenslade 1978; Andersen 1990; 1995). The relative abundances of the different functional groups has been proven to be sensitive to environmental change and provide information on the processes behind the change (Andersen 1990). Previous studies in arid environments, however, suggest that ant communities at the functional group level are quite resilient to changes within such hot, dry and open habitats (Hoffmann 2000; Read and Andersen 2000; Griffin 2001; Hoffmann and Andersen 2003).

As well as the close relationship between ants and plants, patterns within ant communities have been found to correlate with other arthropod and vertebrate groups including Coleoptera, Hemiptera, butterflies, scorpions, Isoptera and lizards in a shrubland habitat (Abensperg-Traun *et al.* 1996). If patterns in ant communities are correlated with patterns in other faunal groups they could be of use as surrogates for the response of a larger section of the ecosystem to ecological change, but this does not appear to be a universal phenomenon (e.g. Major *et al.* 1999).

The specific questions addressed by this study were: do areas with and without shrubs support different arthropod communities? If so, are these differences correlated with floristic, plant structural or soil condition variables? This was assessed at three levels; all arthropods at order level, ants at species level and ants at functional group level. Lastly, do patterns in ant community correlate with patterns in those of other arthropod groups?

3.2 Methods

3.2.1 Study sites

All study sites were located in the plains areas of the central Flinders Ranges. The area receives erratic annual rainfall, averaging approximately 300 mm. The main shrub species on these plains are *Maireana astrotricha* (low bluebush), *M. pyramidata* (black bluebush), and *Nitraria billardieri* (nitre-bush) (nomenclature following Black (1978)). The exotic annual *Carrichtera annua* (Wards weed), is extremely abundant, and dominates the ephemeral herbland areas devoid of perennial shrubs. Various species of *Sclerolaena* and *Danthonia* are among the native species that make up the remaining proportion of the understorey in both open and shrubland areas.

These chenopod shrublands are common within low, winter dominated rainfall areas of temperate Australia, and are susceptible to overgrazing by domestic animals. The plains near Oraparinna in the central Flinders Ranges once supported large areas of chenopod shrubland (Symon 1971); however, the distribution of the perennial shrubs has been greatly reduced since the introduction of sheep in the mid-1800's (Barker 1971). Continued high grazing pressure from goats, rabbits and kangaroos since the removal of domestic stock in 1971 has hampered its recovery. Evidence of past distribution of the shrublands can be seen in the remnant patches of chenopods (Symon 1971), and soil type distribution indicative of this type of vegetation (Lay 1998). Chenopod shrubs are now present only in relatively small patches surrounded by an almost continuous matrix dominated by annual weeds, mainly *C. annua*. The exact cause of the patchiness of the remaining shrub areas is not known but it is likely to be at least partly related to their distance from an historical watering point, around which grazing pressure would have been much greater. Neighbouring sheep stations, such as Wirrealpa Station, have retained large tracts of chenopod shrubland due to a history of more conservative stocking rates.

A total of nine sites were surveyed (Figure 3.1). These included three paired sites within the National Park; within each pair, one site was chosen inside a patch of shrubland (SHRUB), dominated by *N. billardieri* (**P1**, 31° 17.07′ S, 138° 47.75′ E), *M. pyramidata* (**P2**, 31° 20.89′ S, 138° 48.58′ E), or *M. astrotricha* (**P3**, 31° 17.16′ S, 138° 50.01′ E), with the other of the pair at least 150 m from the outside edge of the shrub patch in ephemeral herbland dominated by *C. annua* (HERB). The three other (SHRUB) sites were located on neighbouring Wirrealpa station (**W1**, 31° 20.58′ S, 138° 54.71′ E, **W2**, 31° 20.34′ S, 138° 57.66′ E, and **W3**, 31° 19.77′ S, 138° 59.82′ E). These were separated by at least 1 km, and were all dominated by *M. astrotricha*. Shrub cover (approximately 10-20%) was similar on all SHRUB sites, although P1 had larger, more widely spaced *N. billardieri* shrubs.

Soil type varied from clay to silty loam across the sites and pH varied from 7.7 to 8.7 (Appendix 2). Organic carbon content was generally low and high soil salinity was only evident at the shrub site dominated by *N. billardieri* (P1). No correlation was found between plant floristic composition, or structure and soil variables in this study or previously by Swaby (1971).

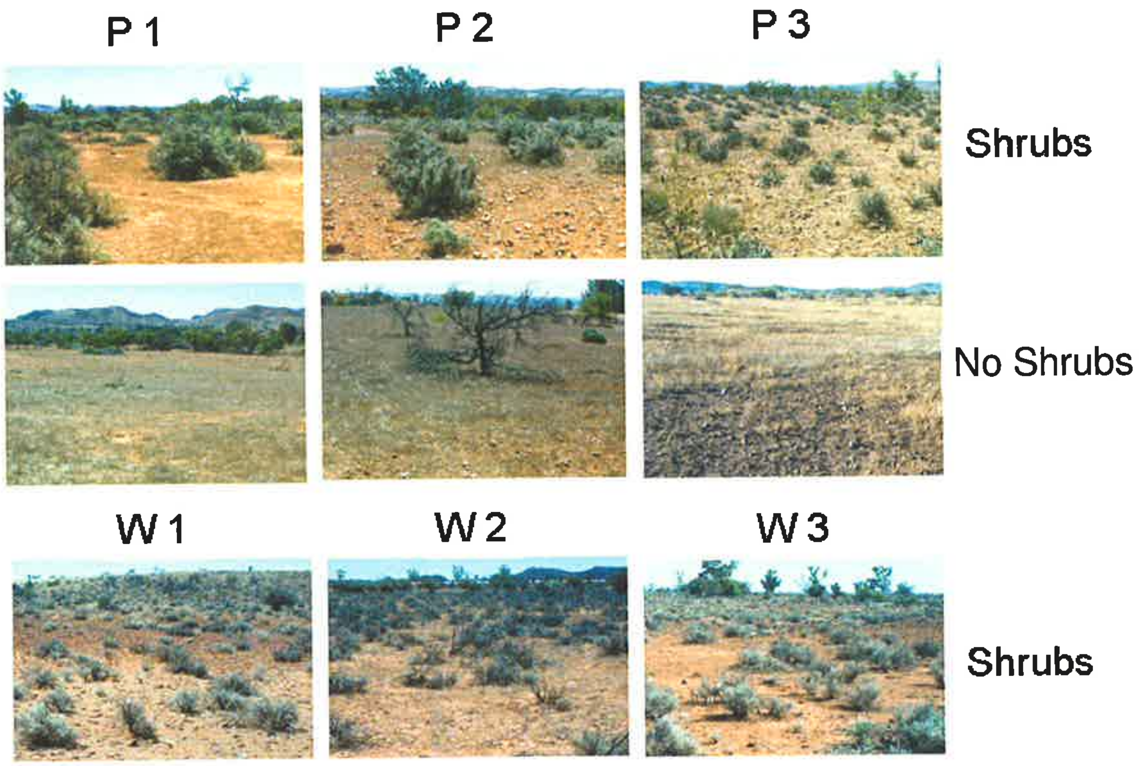


Figure 3.1 Photographs of three paired sites P1, P2 and P3 (with and without perennial chenopod shrubs) within the Flinders Ranges National Park and three sites W1, W2 and W3 with perennial shrubs on Wirrealpa sheep station.

3.2.2 Experimental design

Two 40 m transects of 5 pitfall traps were established at each site in a north-south direction, with traps spaced by 10 m and lines separated by 25 m (Figure 3.2). The traps consisted of 68 mm diameter plastic jars inserted into 75 mm PVC pipe tubes, and were installed with lids 4 weeks prior to sampling to avoid digging-in effects (Greenslade 1973). Immediately prior to sampling, the lids were removed and 50 mL of 50% ethylene glycol and a few drops of detergent were added to each trap. Traps were opened for 5 days in December 2002 during which time the weather was fine and warm with maximum temperatures ranging between 25-32˚C. Light rain occurred on the final day with all sites receiving 0.5 mm. Collecting fluid was topped up as necessary over the 5 days to compensate for loss by evaporation.

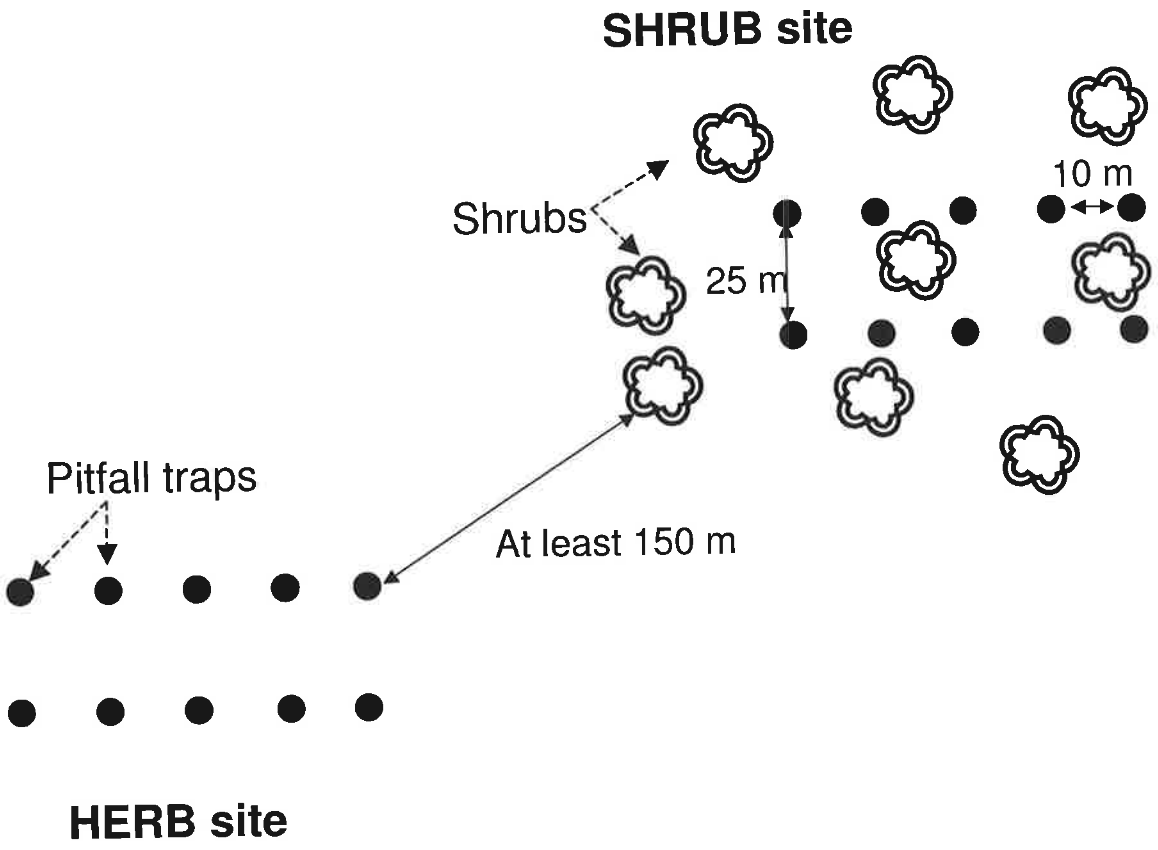


Figure 3.2 Layout of pitfall traps in sites with and without shrubs (herbs only). Not drawn to scale.

Once collected, samples were transferred to 70% ethanol and all arthropods were sorted to order level. Wasps and spiders were identified to family and sorted into morphospecies, while ants were sorted to genus using Shattuck (1999) and then to morphospecies.

To characterise habitat structure, three transects, each 3 m long, separated by 1 m and parallel to the pitfall trap line were surveyed in the vicinity of each individual pitfall trap. Every 5 cm along each transect, the type and height of the highest structure (e.g. litter or plant species) was recorded. If there was no vegetation cover, height was recorded as zero. In total, there were 180 measurements associated with each trap. As this survey was conducted in summer and the area had received very little rain for several months preceding this study, many of the ephemeral herbs, forbs and grasses were dead and could not be identified to species.

The 10 cm deep core of soil removed when the pitfall traps were installed was retained for soil analysis. Air-dried samples from all 10 cores were analysed for particle size using the mechanical analysis method of Gee and Bauder (1986), and electrical conductivity (EC) and pH using a 1:5 soil:water extract (Cass *et al.* 1995) and an EC/pH meter. Three samples were randomly chosen from each site and analysed for organic carbon content using the method of Walkley and Black (1934) and an average obtained for each site.

3.2.3 Analysis

The arthropod and environmental data from each transect were pooled to produce two records from each site. Multivariate analyses of soil variables, vegetation, and arthropod order, ant functional group and ant morphospecies abundances were performed using Non-metric Multidimensional Scaling (NMDS) (Euclidean distance measure) using PC-ORD 4.10 (McCune and Mefford 1999). For some analyses of ant morphospecies the large numbers of a few species were compensated for by converting the entire data set to the abundance classes used by Hoffmann (2000) (1 = 1 ant, 2 = 2-5 ants, 3 = 6-20 ants, 4 = 21-50 ants, 5 = 51-100 ants, 6 = 101-1000 ants, 7 = > 1000 ants) or by using range standardisation, which proportions the abundance data for a species or group across all sites (Andersen and Majer 2004). Multi-Response Permutation Procedures (MRPP), a non-parametric multivariate test for detecting significant differences between groups (McCune and Grace 2002), was used to test for significance of separation of the SHRUB and HERB sites. The Euclidean distance measure was used. Correlation analyses were performed on the average number of ant, spider and wasp species for each site using JMP 4.0.3.

3.3 Results

3.3.1 Arthropod orders

The number of orders represented at sites with shrubs was not consistently higher that those in the HERB sites, although the site where the greatest number of orders was collected was one of the more intact shrubland sites on Wirrealpa Station (Table 3.1, Figure 3.3).

Table 3.1 Numbers of arthropod orders, ant genera and ant, spider and wasp morphospecies collected in ten 68 mm diameter pitfall traps opened for 5 days at each site.

Site	SHRUB/HERB	# orders	# ant genera	# morphospecies		
				ants	spiders	wasps
P1	SHRUB	13	9	24	17	26
P1	HERB	13	10	18	14	11
P2	SHRUB	15	8	16	12	7
P2	HERB	13	9	17	9	8
P3	SHRUB	13	11	17	13	8
P3	HERB	13	8	17	5	16
W1	SHRUB	15	9	17	8	3
W2	SHRUB	12	11	21	13	15
W3	SHRUB	18	10	19	8	6

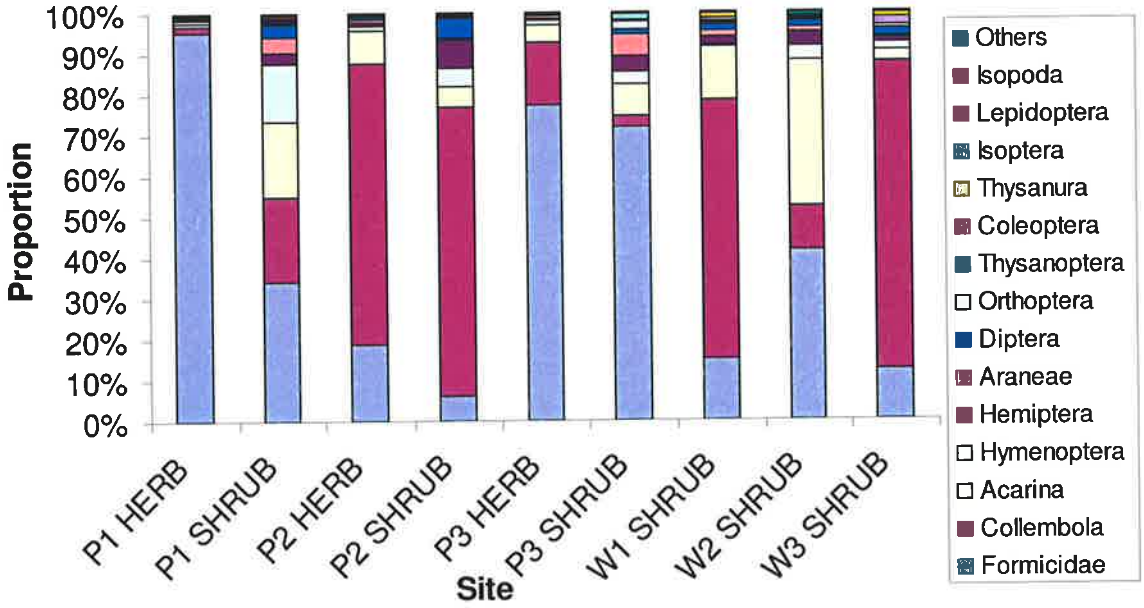


Figure 3.3 Ordinal level composition of the terrestrial arthropod communities at sites in the National Park (P1, P2 and P3) and on Wirrealpa Station (W1, W2 and W3).

3.3.2 Ant community

A total of 57 ant species were collected from the nine sites (Appendix 3). The species collected in the highest numbers was *Iridomyrmex* sp. B. This species was found in very large numbers in two sites but was virtually absent from all others. *Iridomyrmex lividus* was found in much lower numbers but across 7 of the 9 sites. Seven other *Iridomyrmex* species were collected infrequently, making this the second most speciose genus collected after *Melophorus* with 13 species. Species with widespread distributions included *R. metallica*, *Monomorium* sp. B, *Pheidole* sp. B, and *Melophorus* sp. U and sp. J. At functional group level, 7 functional groups were collected across the sites. A high proportion of Dominant Dolichoderines was found in two of the HERB sites; however, this pattern was not evident at the third site. The proportion of Dominant Dolichoderines was low in all sites with shrubs. Other functional groups making up a large proportion of the ant communities were the Hot Climate Specialists, Generalised Myrmicines and Opportunists; however no common patterns were obvious across sites with and without shrubs (Figure 3.4).

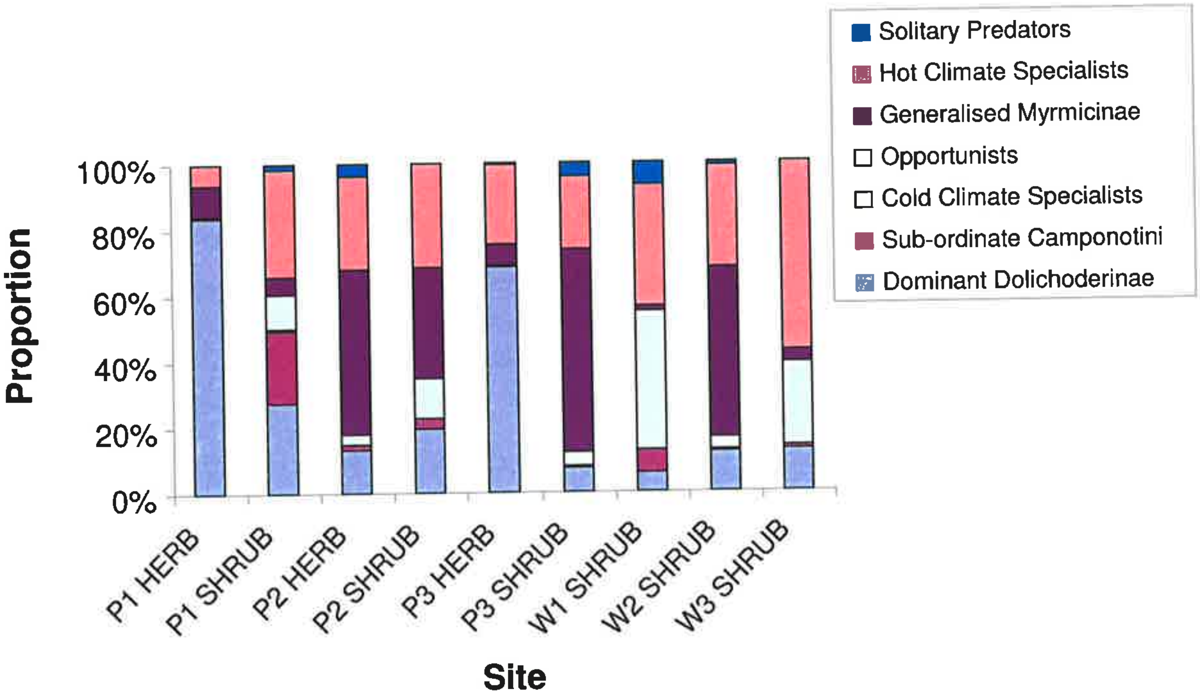


Figure 3.4 Functional group composition of ant community at sites in the National Park (P1, P2 and P3) and on Wirrealpa Station (W1, W2 and W3).

3.3.4 Comparison of ordinal, ant species and functional group responses

A comparison of the total number of orders or ant species at each site indicated no consistent differences between the community composition of shrub and herb sites (Table 3.1). A pattern related to the presence or absence of shrubs was also lacking in the proportional composition of the arthropod orders and ant communities (Figures 3.3 and 3.4).

However, order, ant species and ant functional groups all showed significant grouping by the three types of habitat (National Park sites with shrubs, without shrubs, and shrub sites on Wirrealpa Station) in multivariate comparisons. Further, the difference between groups was consistently greater when divided into the three habitat types than when the sites with shrubs on Wirrealpa station and in the National Park were combined. The separation of the three groups was greatest at ant functional group level (Table 3.2). At order level the pattern among the sites was relatively weak (Figure 3.5). Two of the groups contributing most to the position of the points were ants and spiders but no environmental variables correlated with the abundance of these groups. Increasing soil pH did, however, correlate with the abundance of Orthoptera and Isoptera.

Table 3.2 Multiresponse Permutation Procedure results indicating the degree of separation of the SHRUB and HERB sites in the National Park, or SHRUB, HERB and WIRREALPA sites (greater T statistic value), and homogeneity within groups (greater A value). The significance of the grouping is demonstrated by a p-value.

Analysis	**Group**	**T**	**A**	**p**
Order log	SHRUB/HERB	-4.34	0.104	0.002
	SHRUB/HERB/WIRREALPA	-6.88	0.235	<0.001
Species range standardised	SHRUB/HERB	-4.29	0.100	0.003
	SHRUB/HERB/WIRREALPA	-7.00	0.240	<0.001
F group log	SHRUB/HERB	-5.043	0.148	0.001
	SHRUB/HERB/WIRREALPA	-7.24	0.311	<0.001
F group range standardised	SHRUB/HERB	-4.10	0.16	0.005
	SHRUB/HERB/WIRREALPA	-7.04	0.41	<0.001

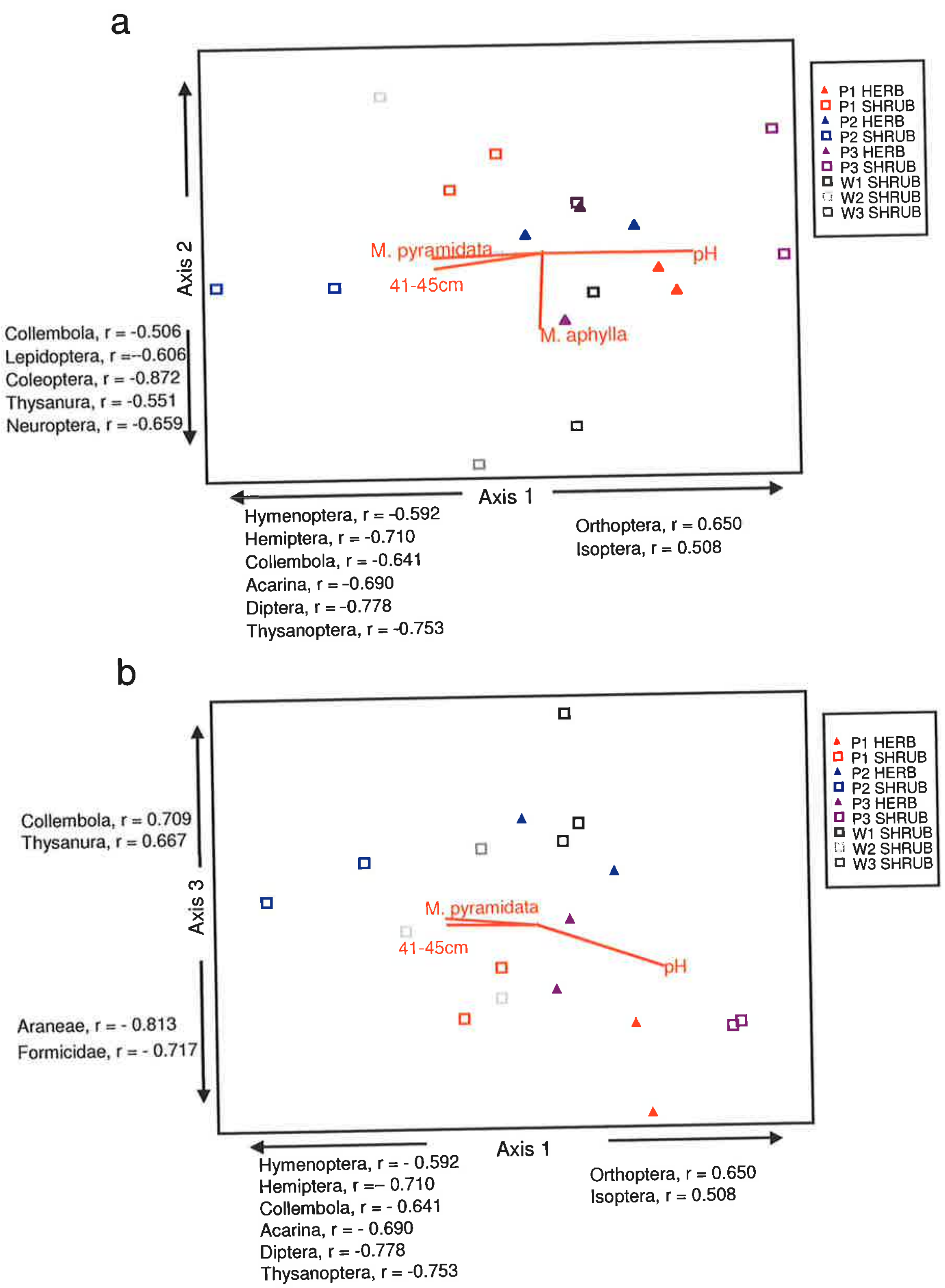


Figure 3.5 Three dimensional NMDS ordination of log (x+1) arthropod order level community data from SHRUB and HERB sites within the National Park and on Wirrealpa Station (stress = 9.83, instability = 0.00008), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Correlations with environmental variables are shown as vectors ($r^2 \geq 0.25$).

At ant species level a degree of separation between sites with and without shrubs was evident (Figure 3.6). The greatest separation of the sites appeared along Axis 3 with the HERB sites grouping together, largely due to greater proportions of *Monomorium* sp. B and *Melophorus* sp. U in their communities. This correlated with an increase in cover of litter and *Carrichtera annua* (Wards weed) and low structure in the vegetation community. The position of the SHRUB sites along that axis can be explained by higher abundances of a number of species, predominantly *Melophorus* sp. P and these communities correlated with more bare ground, cover of *Sclerolaena* spp. and medium height structure of plants.

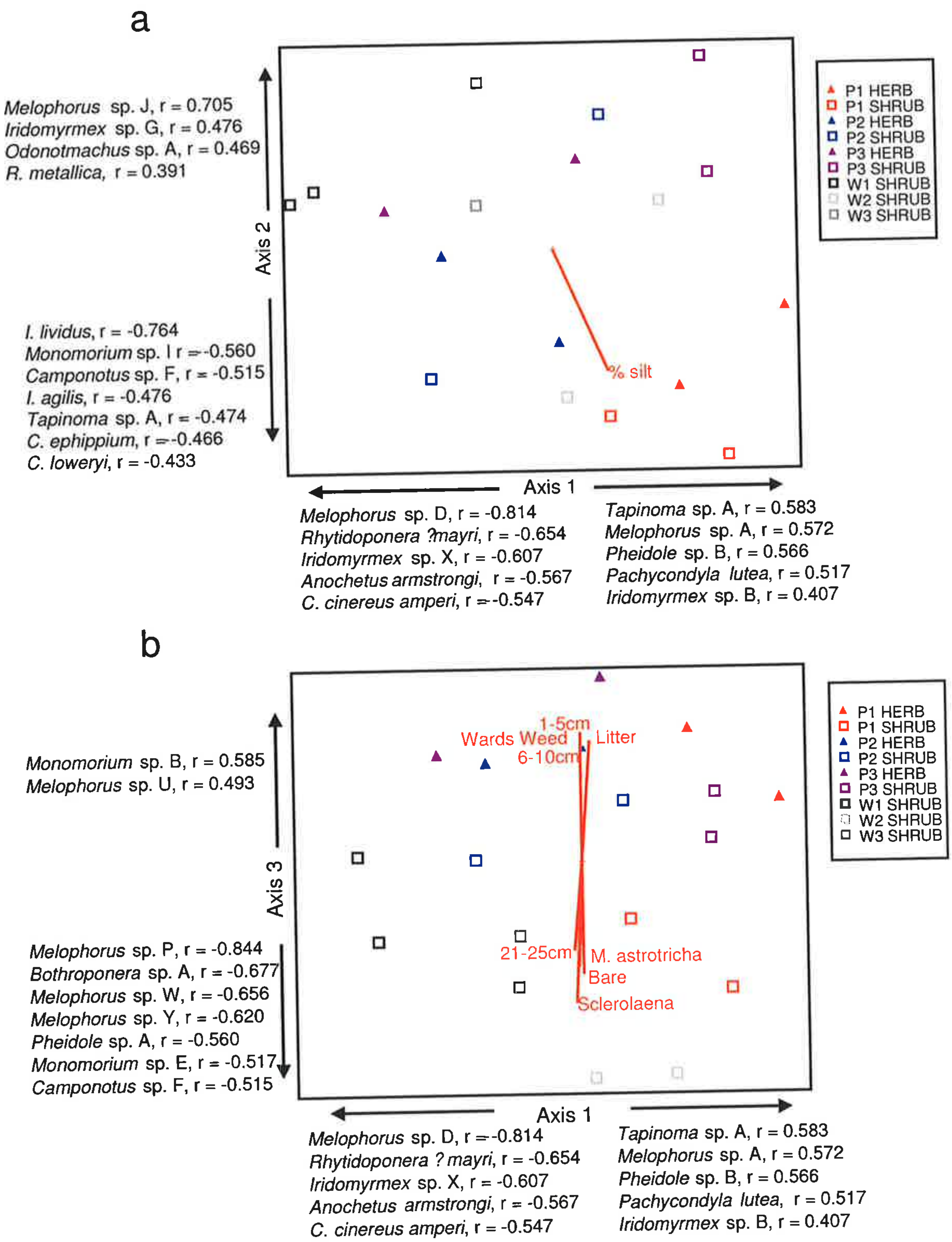


Figure 3.6 Three dimensional NMDS ordination of range standardised ant species abundances from SHRUB and HERB sites within the National Park and on Wirrealpa Station (stress = 13.5, instability = 0.00007), **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Correlations with environmental variables are shown as vectors ($r^2 \geq 0.4$).

The greatest differences in community composition among the three groups can be seen in the log (x+1) ant functional group abundance analysis (Table 3.2). The range standardised functional group data produced the ordination with lowest stress, but the differences between communities in the SHRUB, HERB and WIRREALPA sites were not as great. The patterns produced by the functional group analysis were similar to that for ant species although the correlations with environmental variables were not as strong (Figure 3.7). The position of the HERB sites was explained by higher abundances of Dominant Dolichoderines, Generalised Myrmicines and Hot climate Specialists and correlated again with the cover of litter and *Carrichtera annua*. The SHRUB sites, especially those on Wirrealpa station, had higher proportions of Opportunists and Sub-ordinate Camponotini, and correlated with a greater variation in height of vegetation, more dead annual plants and an increase in exposed rock on the soil surface.

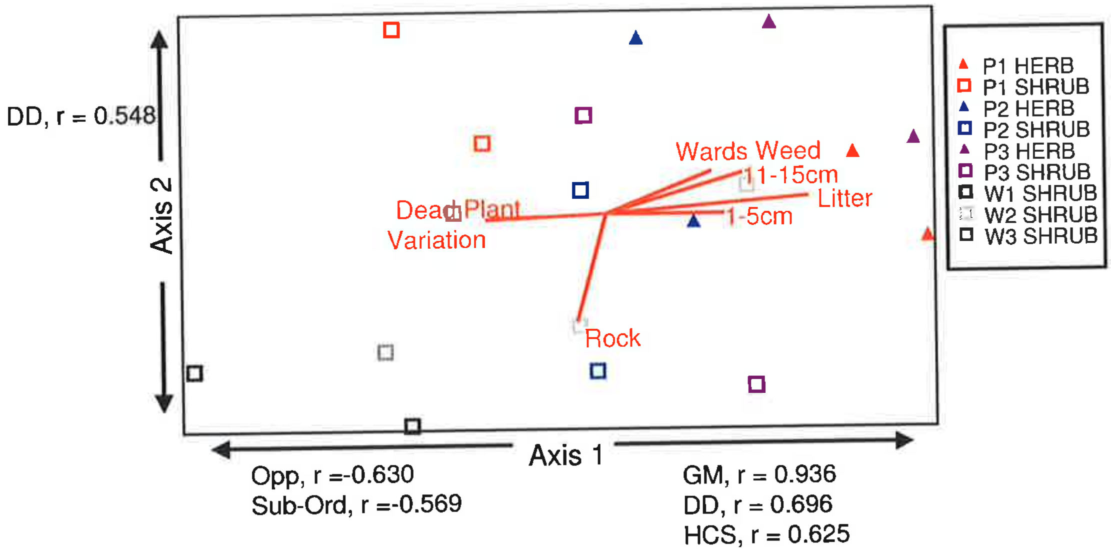


Figure 3.7 Two dimensional NMDS ordination of log (x+1) ant functional group abundances from SHRUB and HERB sites within the National Park and on Wirrealpa Station (stress = 13.75, instability = 0.00008). Correlations with environmental variables are shown as vectors ($r^2 \geq 0.3$). DD = Dominant Dolichoderinae, GM = Generalised Myrmicinae, Sub-Ord = Subordinate Camponotini, SP = Specialist Predators, Opp = Opportunists, HCS = Hot Climate Specialists.

3.3.5 Correlations between species richness of arthropod groups

A positive relationship was found between the species richness of the ant community and that of spiders and wasps collected at each site (Figure 3.8). A similar correlation was also found between spider and wasp species richness (Figure 3.9).

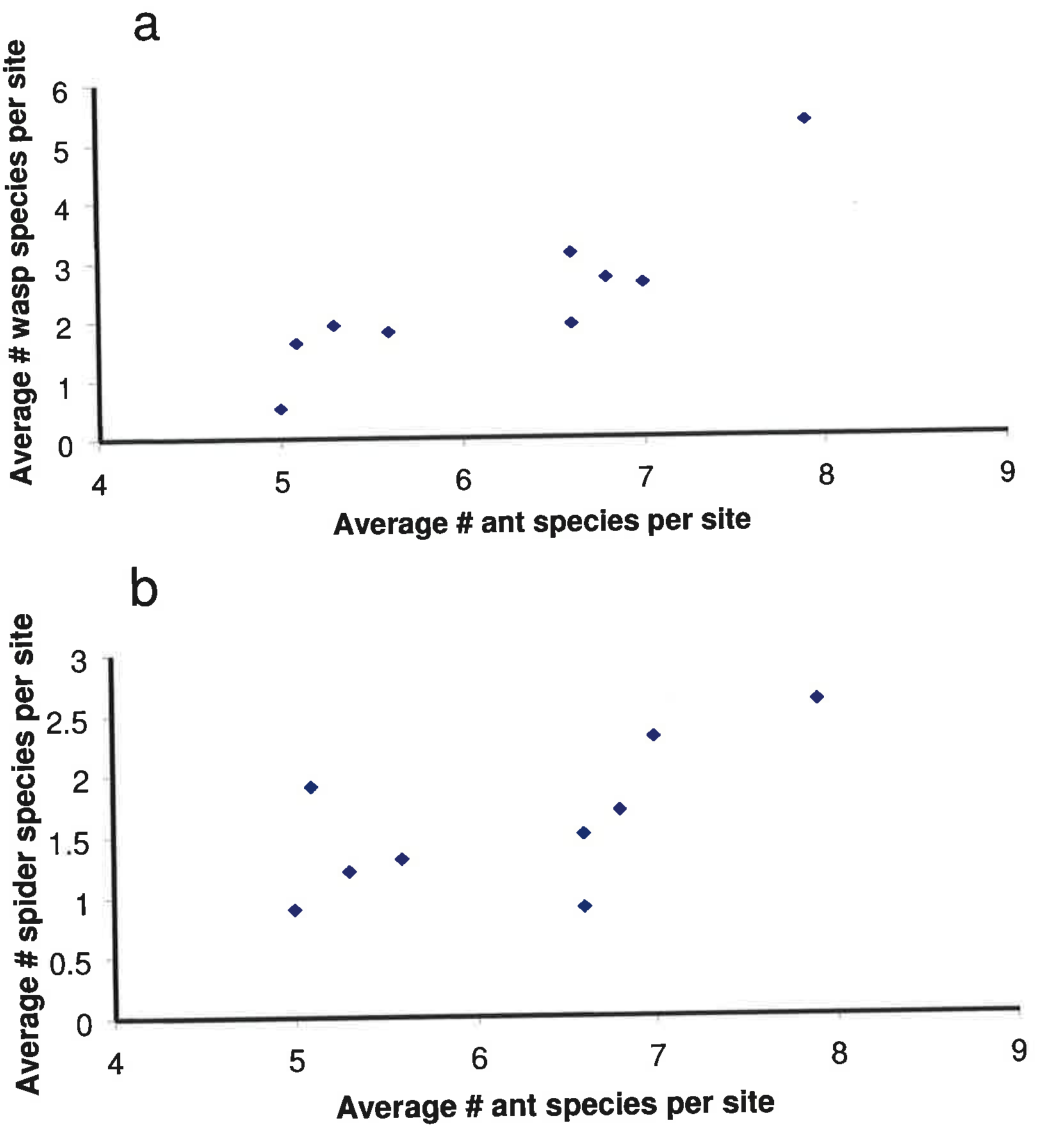


Figure 3.8 Average number of **a)** wasp species ($r^2 = 0.7657$, $p = 0.002$) and **b)** spider species ($r^2 = 0.4099$, $p = 0.0633$) per site against average number of ant species per site.

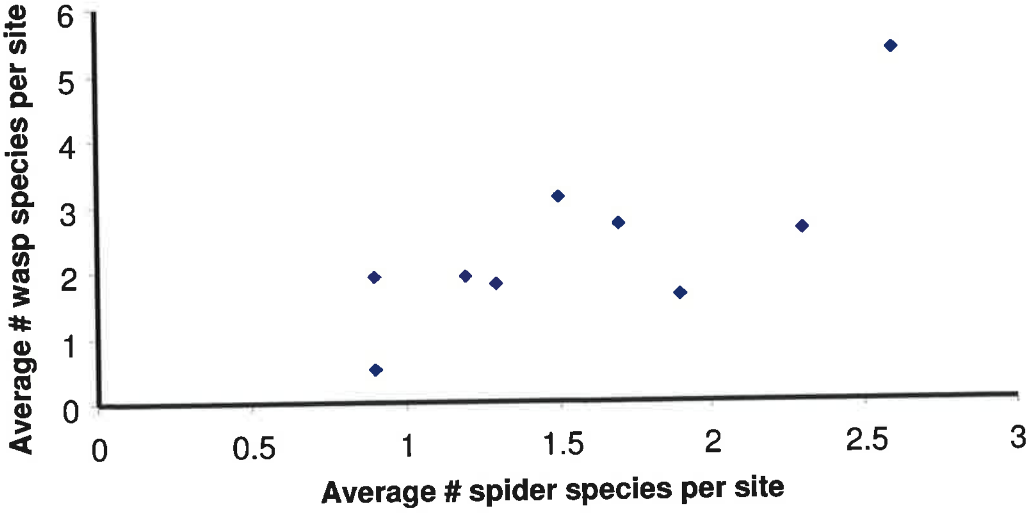


Figure 3.9 Average number of spider species per site against average number of wasp species per site ($r^2 = 0.5805$, $p = 0.017$).

3.4 Discussion

Order level arthropod and ant communities both appear to be responsive to the loss of shrubs within this semi-arid environment. Ant functional groups appear to be most sensitive to the presence or absence of shrubs, however the species level ant community composition was the most clearly linked with the habitat variables measured. Positive correlations of ant species richness with other arthropod groups were also evident.

The considerable variation in the ground-dwelling ordinal arthropod communities among the sites did not closely reflect differences in plant floristic or structural diversity despite other studies finding clear links between these (Majer 1983; Siemann *et al.* 1998; Morris 2000). A time lag in the response of the arthropod community to variation in the vegetation is not likely to be an explanation for this, due to the length of time since the modification of the systems. Closer relationships may have been found if all arthropods had been identified to species level, as responses at this level have been noted in other environments (Siemann *et al.* 1998; Morris 2000) and if a wider cross section of the arthropod community was sampled using a variety of collecting techniques (Romero and Jaffe 1989).

The lack of any relationship with the plant community could also be due to the low floristic and structural diversity in this environment when compared with habitats such as woodlands with diverse understorey species or grasslands. Plant diversity may also have been lower than usual during this study period due to exceptionally dry seasons experienced over the previous two years and the absence of annuals during the dry summer months when this work was undertaken. Annual plants may be an important source of food for herbivores, produce seeds for granivores and harbour other arthropods on which predatory species can prey. A more accurate picture of the role played by the plant community in determining arthropod community structure might be revealed by a survey of plant species richness in spring after a winter of high rainfall.

The differences noted between ant communities in areas with and without shrubs in this environment are in contrast to a lack of correlation observed in other arid or semi-arid environments between ant communities and broad patterns in the plant community (e.g. Whitford *et al.* 1998). This is also contrary to the results of other studies in similar environments that have examined other causes of ecological change, such as the impacts of mining (Read 1996; Hoffmann *et al.* 2000), fire (Hoffmann 2003) and grazing (Landsberg *et al.* 1999; Hoffmann 2000; Read and

Andersen 2000), or active regeneration of native vegetation during minesite rehabilitation (Andersen 1997a; Majer and Nichols 1998). It must be conceded that plant species diversity did not appear to be important to the ant community in this environment and structural diversity *per se* only correlated with the functional group composition of the ant community and with greater abundance of Opportunist and Sub-Ordinate Camponotini, and lower abundance of Dominant Dolichoderines and Generalised Myrmicines. However, other habitat variables such as the proportion of low or medium vegetation height did correlate with ant community composition at both species and functional group levels.

In general, ant functional groups appear to be the most useful level for comparing the differences in ant community composition among sites with and without a shrub overstorey. The greater representation of Generalised Myrmicinae, Hot Climate Specialists and Dominant Dolichoderinae in the sites without shrubs was correlated with the amount of *C. annua* (Wards weed), a plant that is much more abundant in degraded areas without chenopod shrubs and would provide an abundant source of food for seed-eating Generalised Myrmicine ants (Cooke 2003). The short vegetation and litter cover that correlated with ant community structure at these sites were also linked to the cover of *C. annua* as most of the plants in the short height classes belonged to this species and the litter was predominantly dead *C. annua* lying on the soil surface.

The Dominant Dolichoderinae functional group did not correlate with the amount of bare ground or the structure of the habitat in this study, despite a suggestion to this effect from studies in wooded (Andersen 1983) and wetter (Andersen 1986) habitats. Access to bare ground and increased insolation does not appear to be a limiting factor for the behaviourally dominant ant species in this generally hot and bare environment. The abundance of Dominant Dolichoderines did, however, seem to be linked to the cover of *C. annua* but a reason for this is not obvious. The vegetation and soil survey only examined an area within 3 m of the pitfall traps but ants can forage over much larger distances than this. Therefore, it is possible that the environmental variables acting over a larger area need to be examined, so as to encompass the foraging range of the most mobile species.

A possible explanation for the differences noted in the ant communities between the shrubland and herbland sites is the presence of *Acacia victoriae* infested with sap-sucking insects where other shrubs are absent. *Iridomyrmex* species were observed tending these insects, presumably to obtain carbohydrates and water from honeydew. As these species are competitively dominant (Andersen

1992) they can presumably prevent other species from accessing this resource and can use the carbohydrates to fuel their larger colonies. This phenomenon has been observed in rainforests (Blüthgen and Fiedler 2002) but is not as well documented for semi-arid habitats. However, it has been proposed as a general explanation for the high productivity of ants in arid Australian environments (Andersen 2003).

It is unclear why the Hot Climate Specialist ants, and *Melophorus* sp. U in particular, should be in greater numbers in the site without shrubs. Hot Climate Specialists were widespread across all sites and are able to avoid competition with Dominant Dolichoderines by foraging at the hottest times of the day (Andersen 1995), so they are perhaps less influenced by changes within the plant and ant community. While the higher abundance of Opportunists in areas with shrubs may be directly related to habitat structure, it is more likely to be a response to the fact that Opportunists have little competitive advantage over more aggressive ants (Andersen 1995) and Dominant Dolichoderines were less common in the areas with shrubs.

The loss of perennial shrubs appears to have had no apparent effect on ant species richness, but seems to have altered species composition, as found in the semi-arid tropics of northern Australia (Hoffmann 2000). The positive correlation between average species richness of ants and average number of spider and wasp species suggests that patterns in the ant community may reflect those of other arthropod groups and may be of use as a surrogate to monitor their response to ecological change. While it is unclear what common factor might influence the diversity of all three groups, they do share the soil surface: many of the spiders were ground hunting species and most of the wasp species collected were predators or parasitoids of ground dwelling invertebrates (A. Austin pers comm.).

A similar pattern of ant species richness correlating positively with the diversity of other arthropod groups has been found (Majer 1983) but this is the first evidence of such a relationship in a semi-arid habitat (Andersen *et al.* 2004). Studies are needed in similar environments to assess the generality of this association and the usefulness of ants as surrogates for other groups. Many studies have shown a relationship between specific indicator taxa and ecological variables, but their ability to predict the diversity of other taxa has largely gone untested (Cranston and Trueman 1997). The pitfall traps used here were not specifically designed to collect flying insects such as wasps, and these traps did not collect web-building spiders. Other collecting techniques should therefore be employed in future to investigate whether these correlations extend more widely to the wasp and spider assemblages.

In conclusion, these results suggest that broad patterns within the vegetation community such as the presence or absence of shrubs are reflected in the arthropod and ant communities, especially at ant functional group level, but that finer scale patterns relating to plant floristic and structural diversity are less evident. It is therefore suggested that the plant community is not an adequate surrogate for the response of the arthropod community in this semi-arid shrubland. The species richness of the ant community may, however, reflect that of other arthropod groups. The results of this study also suggest that in semi-arid shrubland environments attempts to find correlations between ant community structure and the plant community should take into account a much wider area than used here.

CHAPTER 4: RESPONSE OF SPIDER AND ANT COMMUNITIES TO INCREASED HABITAT STRUCTURE IN A SEMI-ARID HABITAT.

4.1 Introduction

Habitat structure plays an important role in structuring fauna communities and this appears to be particularly important for arthropod communities (May 1978; Southwood 1978). In some instances habitat structure can have large impacts on animal communities irrespective of plant species richness (MacArthur and MacArthur 1961), while in other situations biological interactions are equally important and the availability of suitable habitat is not enough to explain species diversity on its own (Connell and Orias 1964). Spiders are one group that may be much more strongly affected by plant structure than other biological regulatory factors such as prey availability (Greenstone 1984).

The composition of spider communities has been shown to be closely tied to the structure and cover of vegetation, as they use it for habitat, attaching webs and egg cocoons, hunting for prey (Marc *et al.* 1999) and dispersal via ballooning (Duffey 1978). The abundance of spiders has been shown to increase within a habitat when structural complexity (e.g. shrub size) increases (Abraham 1983; Greenstone 1984; Halaj *et al.* 1998), and decline as complexity decreases through grazing (Luff and Rushton 1989; Gibson *et al.* 1992). The species diversity of spiders has been correlated with various measures of habitat complexity including the tip height of vegetation (Greenstone 1984), twig biomass of forest trees (Halaj *et al.* 1998), and depth of litter layer and rigidity of plant structure (Gibson *et al.* 1992).

The community composition of spider communities also appears to be sensitive to changes in habitat complexity within an environment, as different assemblages of spider species tend to inhabit different strata of the vegetation (Abraham 1983). Dividing the spider community into functional groups according to their method of catching prey has allowed the specific habitat preferences among species to be explored (Hatley and MacMahon 1980; Robinson 1981; Bultman and Uetz 1982; Scheidler 1990; Halaj *et al.* 2000). For example, large web spinners appear to prefer the shrub layer (Abraham 1983), and are therefore most susceptible to the loss of tall structure through grazing (Gibson *et al.* 1992), while ambush predators prefer the herb layer, and wandering predators the ground surface (Gibson *et al.* 1992).

If the overstorey vegetation layer is removed from a habitat through overgrazing or other actions, species dependent on the above-ground structures of plants obviously cannot survive (Morris 2000), but many spiders have the ability to rapidly colonise new structures if the shrub layer is restored, for example through ballooning (Gibson *et al.* 1992; Mrzljak and Wiegleb 2000) and walking (Mrzljak and Wiegleb 2000).

Generally, few studies have addressed aspects of vegetation structure in successional systems (Morris 2000). During colonisation of mine rehabilitation sites, the number of species of spider increased and was highest in sites with most dense vegetation, regardless of age or vegetation type (Mrzljak and Wiegleb 2000). The community composition also alters as plant succession progresses, with species that prefer open areas being excluded when vegetation became thick (Mrzljak and Wiegleb 2000). In contrast, Hurd and Fagan (1992) found a decrease in spider species richness with succession from herbland to woodland. However, this study used only pitfall traps and the decrease may have been due to generalist species that inhabited the litter and ground layer moving into more complex vegetation as it became available, while any changes in the above ground community went undetected.

Canopy structure is also thought to be the most important habitat variable affecting ants, albeit indirectly, through the influence of plant structure and litter on the insolation of the soil surface (Andersen 1982, 1983). However, little experimental evidence is available for the importance of shade and litter to semi-arid ant communities, especially in environments where litter and shade are extremely limited.

This study aims to assess the impact of an increase in structural complexity of vegetation on the spider and ant community of a semi-arid ephemeral herbland in the Flinders Ranges through the addition of artificial "plants" of similar structure to a small chenopod shrub. The addition of these structures simulates one aspect of the restoration of the ephemeral herbland to an open shrubland. Under natural conditions of habitat restoration and succession the importance of the availability of structure may be masked by other factors such as resource availability, competition and predation (Gunnarsson 1990). Using plastic plants uncouples the effects of architecture, from plant species diversity, thereby eliminating the possibility of plant species composition affecting the availability of resources either directly or indirectly for spiders. For example, plastic plants are not likely to attract herbivorous arthropods and so are less likely to affect prey availability. The artificial structures therefore allow the importance of this 'non-trophic effect' (Halaj *et al.* 2000) to be tested. This approach has been successfully used in marine environments to uncouple the effects on fish of availability of shelter from food supply related to habitat structure (e.g. Laegdsgaard and Johnson 2001). Plastic plants are likely to have a positive effect on the spider community as they provide spiders with structure on which to build their webs, hide from predators, and provide a vantage point from which to locate and observe prey. They are also likely to have an effect on the microclimate of the immediate area, as they allow escape from the heat of the ground. The shade they produce may also affect the ant community by altering microclimatic conditions through the provision of shade. The design of this experiment also allows for the separation of the effects of an increase in the complexity of the habitat from changes in the abundance of structures, as the number of structures is held constant within each treatment and only the complexity of the structure varied, which has rarely been achieved in other studies.

The questions addressed in this part of the study were: does an increase in structural complexity increase spider abundance and/or species richness in this ephemeral herbland? If so, how does the increase correlate with the complexity of the structures? Are increases in the abundance and/or species richness of web-builder and foliage forager spider functional groups greater than in other groups? Does an increase in structural complexity increase ant abundance and/or species richness in this ephemeral herbland?

4.2 Methods

4.2.1 Study site

The chosen site was in an ephemeral herbland dominated by the introduced annual *Carrichtera annua* (Wards weed) (31° 17.24'S, 138° 50.44'E). This area once supported a low shrubland dominated by chenopod species but over grazing by domestic stock has lead to the total loss of the shrub overstorey (Symon 1971). Despite their low plant species and structural diversity, the herblands still support a relatively large number of arthropod species, including an array of ants and spiders. The spider community consisted mainly of ground hunting species, as the only perennial structure available to web building spiders was the fresh and dried stems of annual plants such as *C. annua* and a few sparse *Acacia victoriae* shrubs. The majority of the vegetation structure was less than 15 cm above the ground. The predominant soil type is a poorly structured red-brown calcareous loam (Swaby 1971). Annual rainfall is highly variable and usually below 300 mm.

4.2.2 Experimental Design

Three blocks of 16 plots (5 x 5 m each) were established in the ephemeral herbland. Approximately 200 m separated Block 1 from Block 2 and 100 m separated Block 2 and 3. The difference in separation of the blocks was necessary to ensure that individual ant colonies were unlikely to forage in more than one block and enough flat, relatively undisturbed ground was available for each block (Figures 4.1-2). In July 2003 six plots from each block were randomly selected. Of these 18 plots, 6 plots were left as controls, while the structural complexity was increased in the others using artificial shrubs arranged randomly within the plots. The remaining 12 plots were divided equally and received nine artificial shrubs of one of two sizes. These were created by combining different numbers of identical plastic Christmas tree segments (thin plastic leaves on a wire base), with three segments being used for the simple plants (simple) and nine for a more complex structure (complex). Each segment had 3 branches of leaves with a maximum length of 25 cm. These were wired together and the branches fanned out to produce a small shrub shape. A steel rod was attached to the base with wire and this was inserted in the ground so that the base of the branches stood 5 cm from the ground and the overall height was approximately 30 cm and diameter approximately 25 cm (Figures 4.3-4).

The 30 unallocated plots within the three blocks were used for the addition of shade experiment (Chapter 5). The 25 m between each plot was thought to be sufficient to minimise interference between the two manipulations.

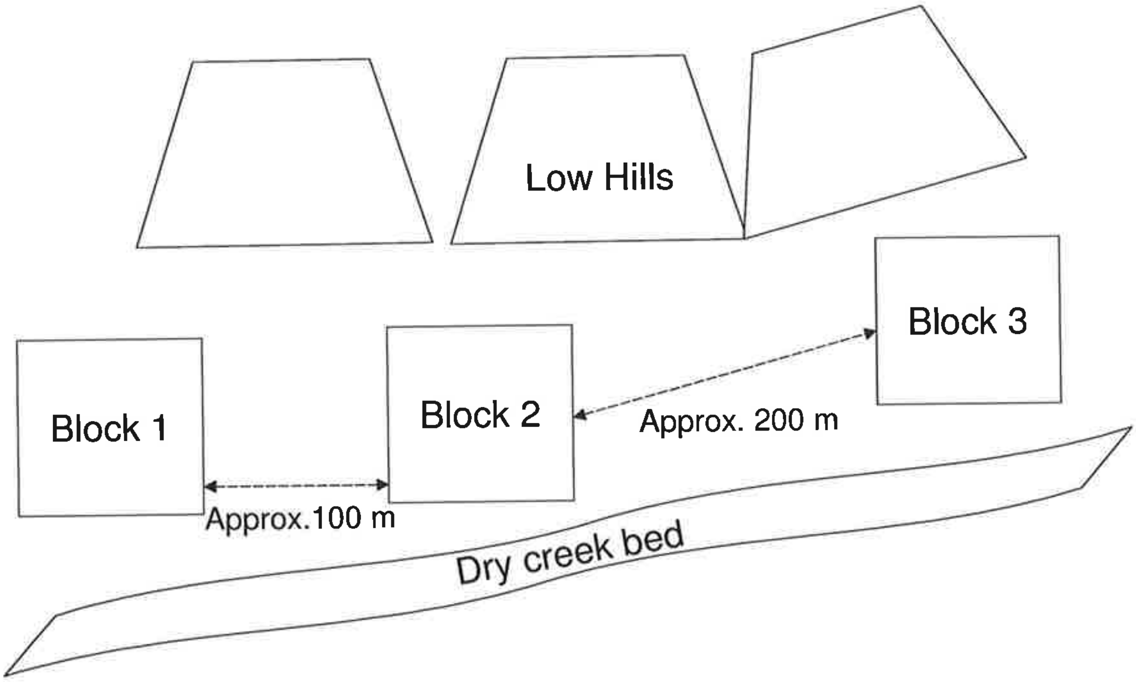


Figure 4.1 Arrangement of experimental blocks within the ephemeral herbland site. Not drawn to scale.

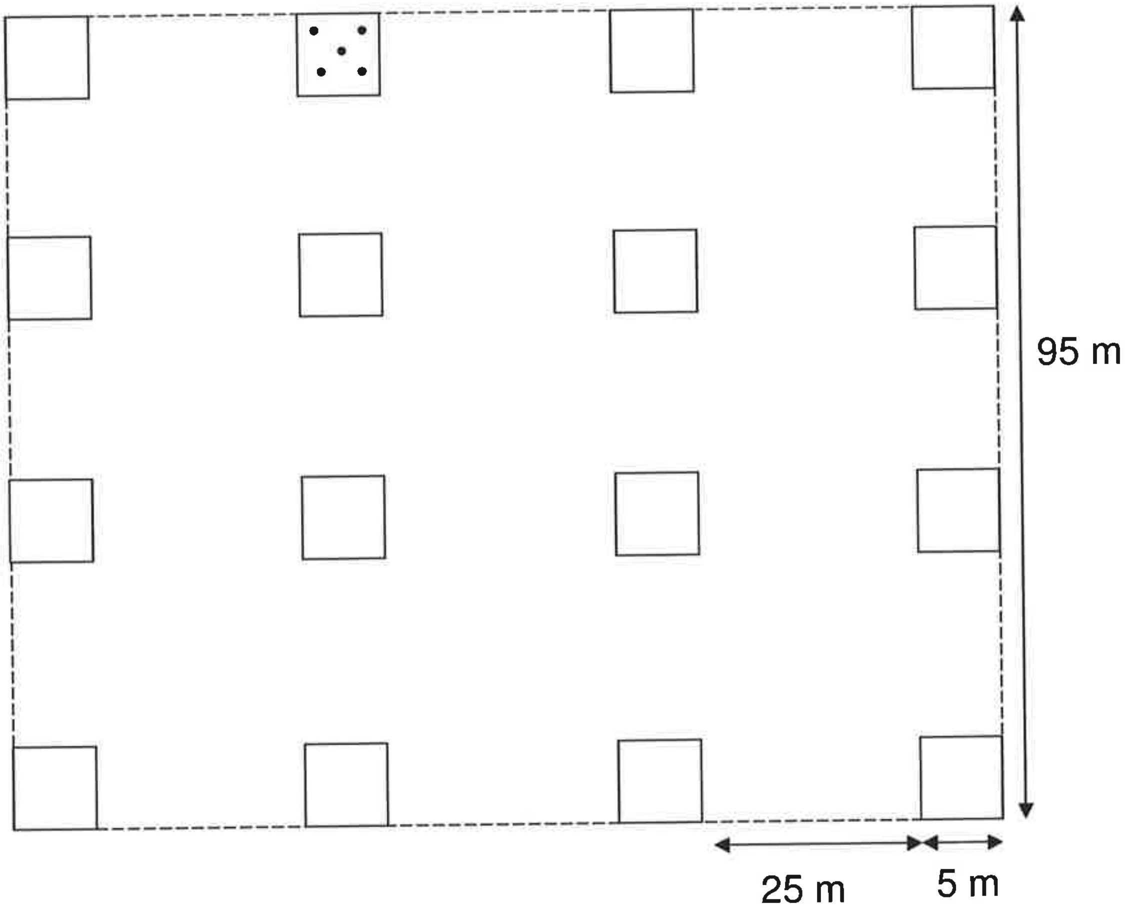


Figure 4.2 Plot and pitfall trap layout within experimental blocks. Small squares represent plots and black circles pitfall trap locations.

Figure 4.3 Small size (simple) artificial plants in ephemeral herbland. Photo taken in December 2003.

Figure 4.4 Large size (complex) artificial plants in ephemeral herbland. Photo taken in July 2003. N.B. Note the increase in surrounding weeds compared with Figure 4.3.

Each 5 x 5 m plot contained 5 pitfall traps in a star design, one in the centre and four radiating to the corners of the plot, 2.5 m from the centre (Figure 4.2). Each pitfall trap consisted of a 68 mm diameter plastic specimen jar inside a 75 mm PVC pipe. Approx 50 mL 50% ethylene glycol (1.5 cm depth) was added to each jar along with a couple of drops of detergent to reduce the surface tension. The traps were opened for 48 h from Tuesday 3rd to Thursday 5th December 2002, during which time the weather varied between a maximum of 25-27 °C. Traps were opened again for 48 h 12 months later between 8th and 10th December 2003 (Temperature maximum range 32-41 °C); 5 months after the plastic plants were installed.

Pitfall traps have limited use for sampling spiders (Topping and Sunderland 1992; Harris *et al.* 2003). Therefore, this study used pitfall traps in conjunction with beating of the plastic plants. During the beating procedure, the structures were carefully removed from the ground and beaten into a white plastic photographic tray. Spiders collected in the tray were then transferred to a collecting jar. The structure was also then inspected for any remaining invertebrates. Pitfall trap and beating collections were made in December 2003.

Specimens were transferred to 70% ethanol. All collections were sorted to order, ants to genus and morphospecies, and spiders to family, morphospecies and functional group. Morphospecies identifications and family placement were verified by D. Hirst (South Australian Museum) and Dr. M.S. Harvey (Western Australian Museum). The use of family level taxonomy has been suggested for spiders to overcome problems associated with the paucity of species level taxonomic knowledge, the large number of rare taxa (Churchill 1997) and to allow the inclusion of juveniles in the data (New 1999). Spider voucher specimens have been deposited in the South Australian Museum, while the ant vouchers are housed at the Waite Insect and Nematode Collection (WINC), Waite Campus, The University of Adelaide. Information on this collection is available from the WINC website www.sciences.adelaide.edu.au/research/winc/.

4.2.3 Analysis

Spiders were assigned to two different types of functional groups based on their mode of catching prey and their habitat preference following current biological knowledge of each family (M. Harvey pers comm., Main 1976; Austin 1980; Hawkeswood 2003). A spider was placed in either the 'Web Builders' or 'Active Hunters' group and the same spider was then assigned to either the 'Foliage Hunting', 'Ground Hunting' or 'Both' (for those that hunt in both areas). Morphospecies richness was also calculated. Differences in spider species richness and abundances between 2003 and 2002 were also calculated.

Non-parametric Kruskal Wallis tests with blocking were used to test for differences between catches of spiders in pitfall traps among all treatments and overall differences between simple and complex tree plots (control plots were not included because no web building spiders were found there). Tukey HSD post-hoc tests were used to determine how the groups differed from each other. Ant data were analysed using ANOVA. All statistical analyses were performed using JMP (Version 4.0.3).

Multivariate analyses of the spider family level data from 2003 were performed using Non-metric Multidimensional Scaling (NMDS) (Sorensen's Distance measure) using PC-ORD 4.10 (McCune and Mefford 1999). Multi-Response Permutation Procedures (MRPP), a non-parametric multivariate test for detecting significant differences between groups (McCune and Grace 2002), was used to test for significance of separation of the three treatment types.

4.3 Results

Both spiders and ants were collected in relatively high abundance in the pitfall traps. Spiders were also collected from the plastic trees by beating, along with a small number of other arthropods including weevils (Coleoptera), bugs (Hemiptera), cockroaches (Blattodea), mites (Acarina) and a single species of ant (Formicidae).

4.3.1 Spiders

A total of 52 spider species were collected from the pitfall traps and the plastic plants, comprising 16 families (Appendix 4). Seventy-two percent of specimens collected were juveniles.

The total abundance of spiders collected in the plots with complex structure in 2003 was significantly higher than in the control plots (Figure 4.5a) and there was also a significantly greater increase in abundance in the complex plots over the two years. Overall there was in increase in spider abundance in all plots from 2002 to 2003 (Figure 4.5b).

There was a significantly greater increase in spider abundance in the complex plots than the simple plots ($\chi^2 = 6.68$, DF = 2, p = 0.01, complex mean = 12, simple mean = 5.83), but the pitfall trap samples were not significantly different in 2003 or in relation to changes over time (Figure 4.5c).

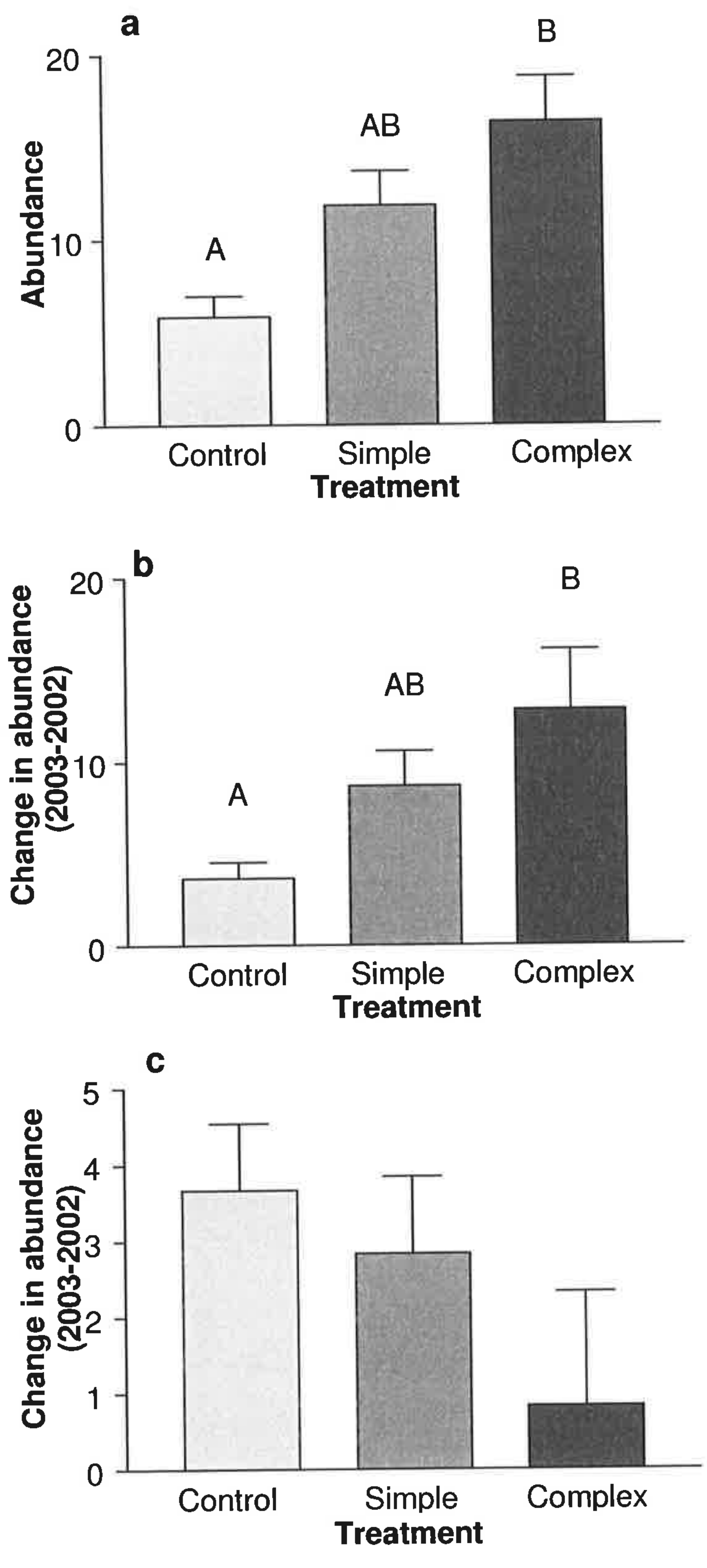


Figure 4.5 a) Total spider abundance in plots with simple, complex or no plastic plants (+/- SE) pitfall and plant data are pooled ($\chi^2 = 9.55$, DF = 2, p = 0.008), **b)** change in abundance from 2002 to 2003 (+/- SE) pooled data ($\chi^2 = 6.88$, DF = 2, p = 0.032) and **c)** change in abundance for pitfall trap data only (no significant difference p>0.5). Letters above are groupings from Tukey-Kramer post-hoc test and indicate significantly different groups (p<0.05).

The addition of artificial structure also increased the species richness of the spider community (Figure 4.6a). Although species richness in the pitfall trap catches in 2003 did not differ significantly, the combined species richness from both pitfall traps and plants did, with the control sites displaying significantly lower species richness than the other plots. The total species richness was higher in the complex plots than the simple plots, but this difference was not significant. When the change in species richness was analysed, the complex plots revealed a significantly greater change in the number of species present than the control plots, with the simple plots being intermediate (Figure 4.6b).

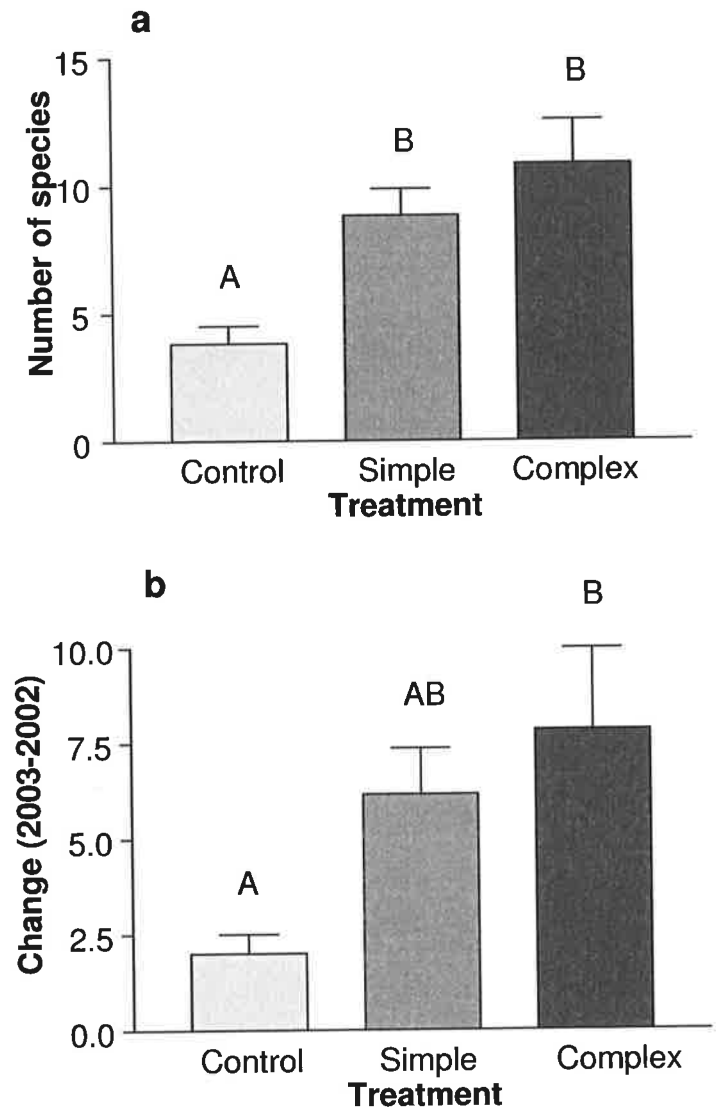


Figure 4.6 a). Species richness of spiders collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 9.84$, DF = 2, $p = 0.007$) and **b)** change in spider species richness in plots with simple, complex and no plastic plants from 2002 to 2003 (+/- SE). Pitfall and beating data are pooled ($\chi^2 = 6.34$, DF = 2, $p = 0.042$). Letters above are groupings from Tukey-Kramer post-hoc test and indicate significantly different groups ($p<0.05$).

The number of spider families represented in the total catches of the simple and complex plots was higher than for the controls but there was no significant difference between the two treatment plots (Figure 4.7a and b).

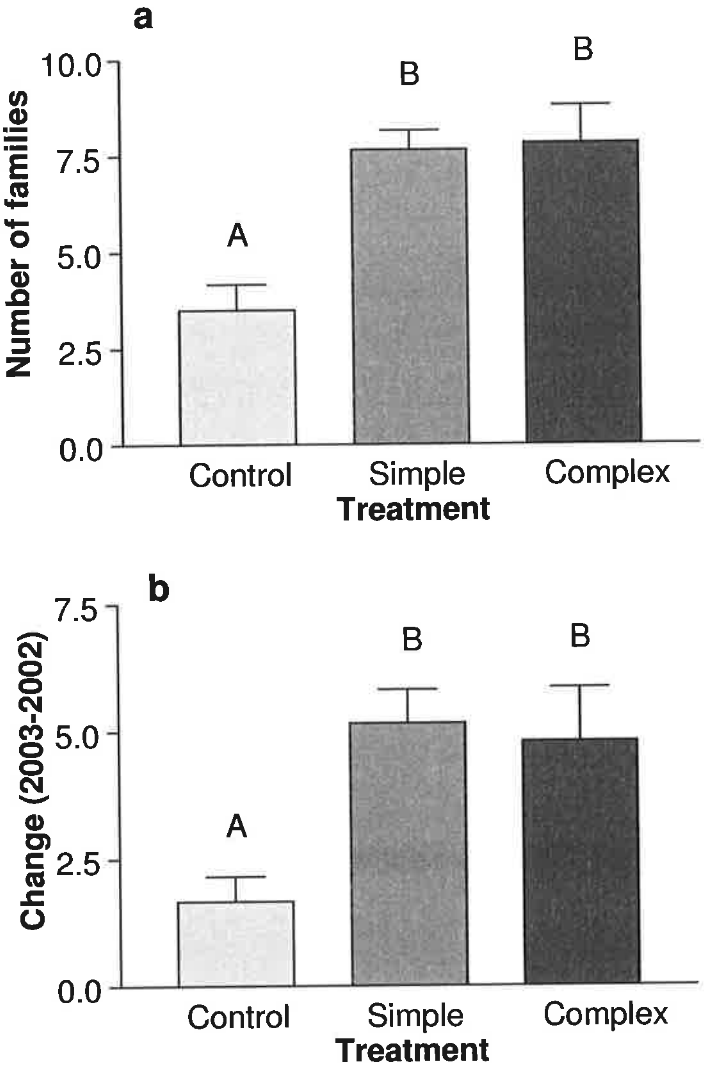


Figure 4.7 a) Number of spider families collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 10.05$, DF = 2, p = 0.007) and **b)** change in number of spider families collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) ($\chi^2 = 8.95$, DF = 2, p = 0.011).

Nine of the 16 families collected in this study showed significant responses to the treatments (Table 4.1). More Araneidae, Corinnidae, Dictyindae and Zoridae were collected in plots with complex plants added. While greater numbers of Clubionidae, Salticidae, Theridiidae and Zodariidae were found in the simple plots. The Gnaphosidae were in greater numbers in both the simple and the complex plant plots compared with the control plots.

Table 4.1 Total spider abundance in each family in 2003 when compared by treatment using Kruskal Wallis/Chi Squared test. Only those with significant results are shown.

Family	χ^2	**p**	**Result**
Araneidae	10.59	0.0050	Complex>Simple and Control
Clubionidae	12.51	0.002	Simple>Complex and Control
Corinnidae	9.19	0.01	Complex>Control
Dictynidae	10.59	0.005	Complex>Simple and Control
Gnaphosidae	11.64	0.003	Simple and Complex>Control
Salticidae	7.63	0.022	Simple> Control
Theridiidae	10.74	0.005	Simple>Complex and Control
Zodariidae	11.26	0.004	Simple>Complex and Control
Zoridae	9.64	0.008	Complex>Simple and Control

The abundance of web building spiders was higher in both the simple and complex plots than in the control plots (Figure 4.8a), as was the change in abundance (Figure 4.8b). A significantly greater number of web-building spiders were collected from the complex plants than the simple plants (Figure 4.8c). However, when the pitfall trap data alone were analysed there was no significant difference. Very similar patterns were observed for the actively hunting spiders (Figures 4.9a-c). There was a significant block effect for active hunting spiders collected from plants, but not in any other comparisons.

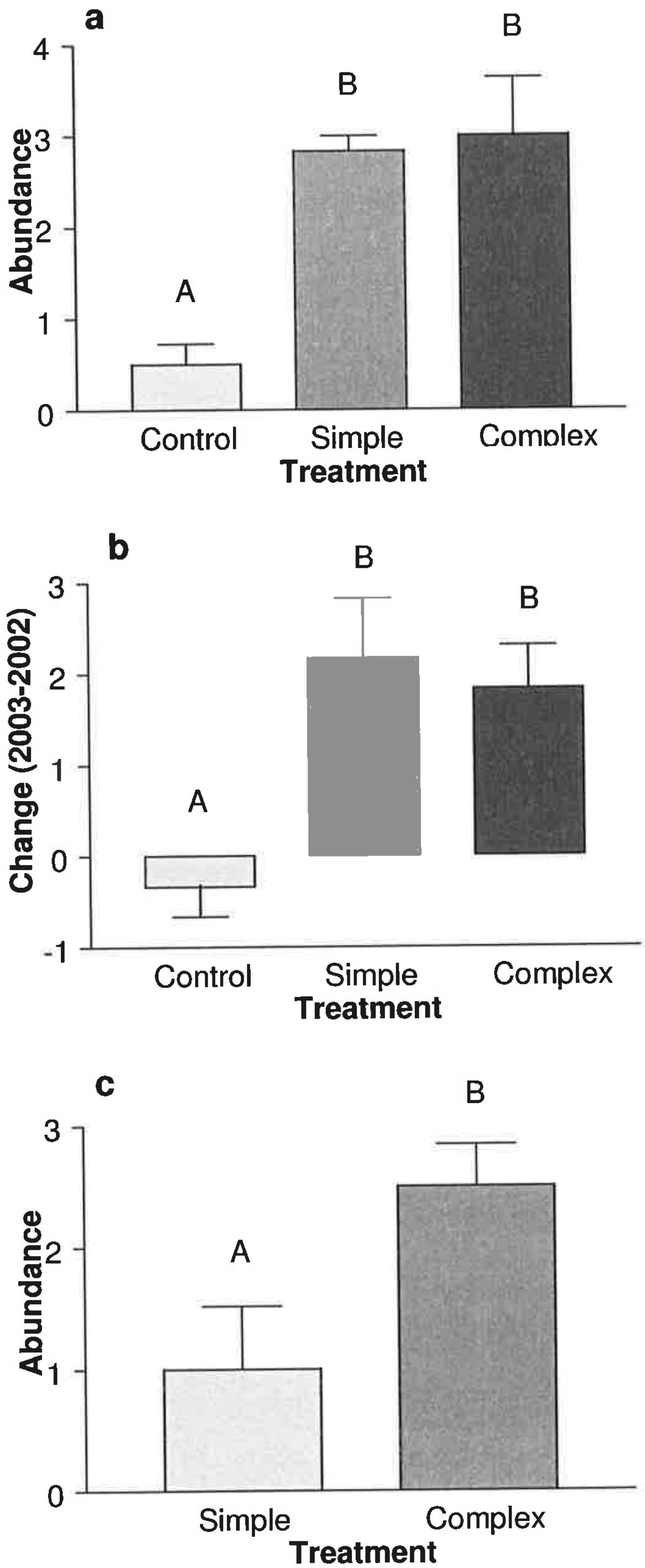


Figure 4.8 a) Abundance of web building spiders collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 9.44$, DF = 2, p = 0.009), **b)** change in abundance of web building spiders collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) ($\chi^2 = 7.91$, DF = 2, p = 0.019) and **c)** abundance of web building spiders collected from plants only in 2003 ($\chi^2 = 4.06$, DF = 1, p = 0.044).

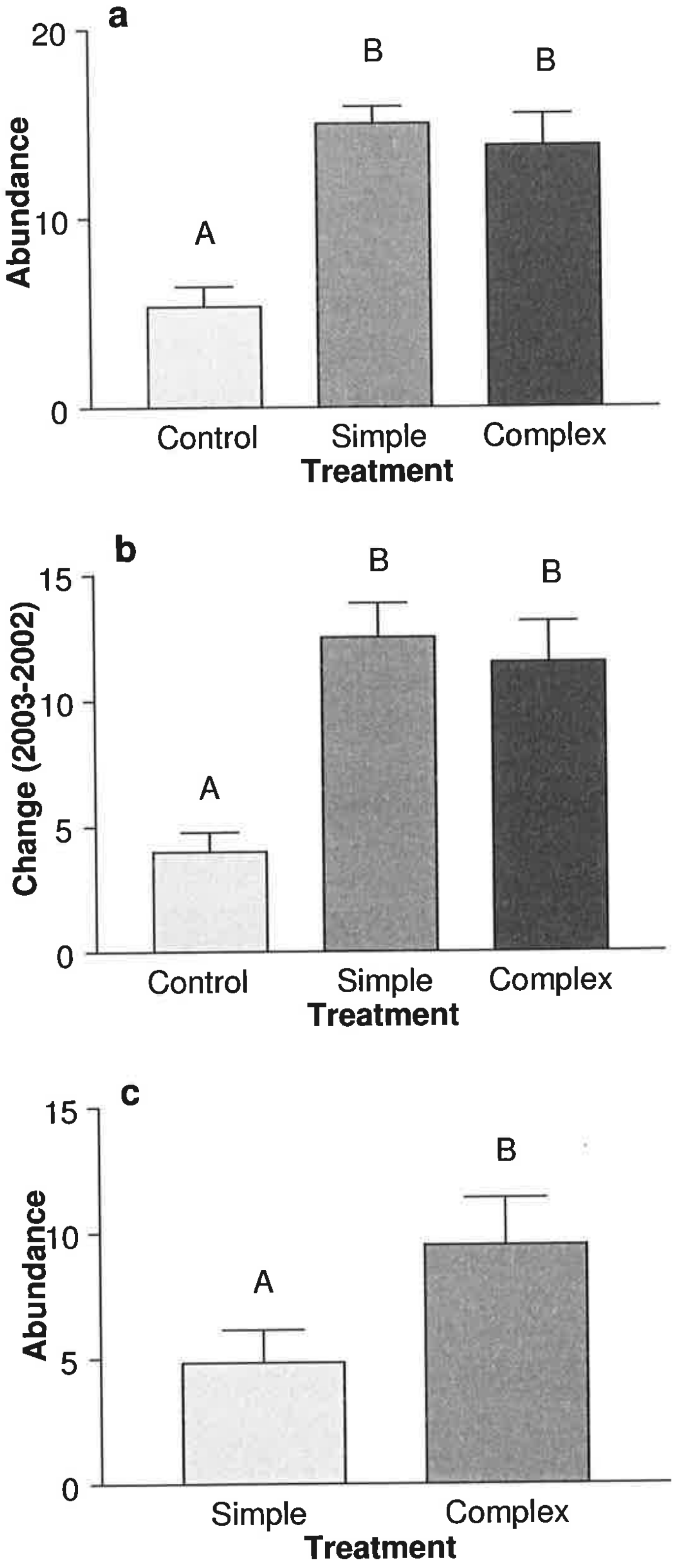


Figure 4.9 a) Abundance of active hunting spiders collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 10.63$, DF = 2, p = 0.005), **b)** change in number of active hunting spiders collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) ($\chi^2 = 11.47$, DF = 2, p = 0.003) and **c)** abundance of active hunting spiders collected from plants only in 2003 ($\chi^2 = 6.68$, DF = 2, p = 0.01).

The number of foliage foraging spiders was greatest in the plots with simple structure (Figure 4.10a), with a similar pattern evident in the analysis of change in abundance over time (Figure 4.10b). However, when the collections from the plants alone were analysed, the complex structure plots had a greater number of foliage foraging spiders but the difference was not significant (Figure 4.10c). The spiders that were known to forage both in foliage and on the ground appeared to respond in the same way (Figures 4.11a-c). There was a significant increase in the number of ground foraging spiders found in the plots with structure added than in control plots in the 2003 data only (Figure 4.12a), and the same pattern was also seen in the change in abundance over the two years (Figure 4.12b). When the ground forager samples from the plants only were analysed, the complex trees contained significantly greater numbers than the simple trees (Figure 4.12c).

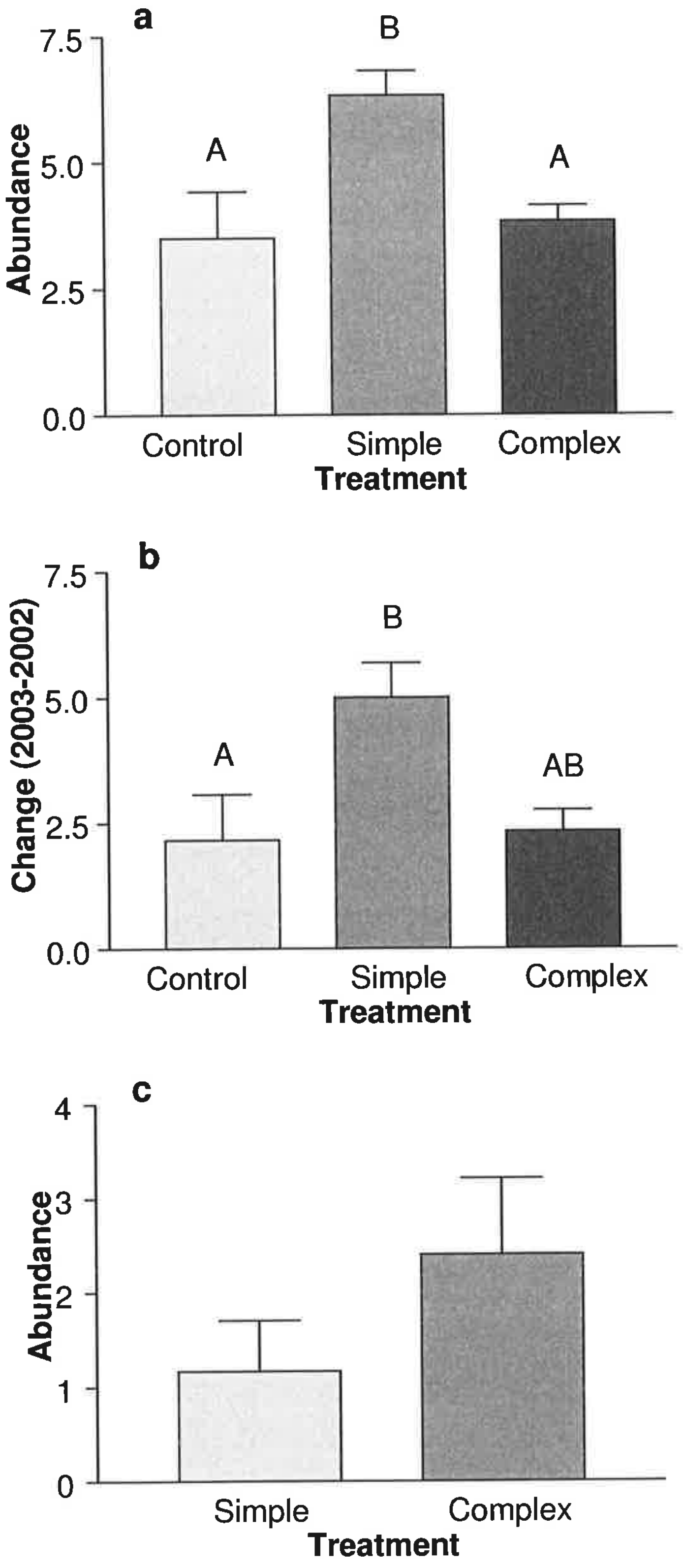


Figure 4.10 a) Abundance of foliage foraging spiders collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 8.85$, DF = 2, p = 0.012), **b)** change in number of foliage foraging spiders collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) ($\chi^2 = 6.43$, DF = 2, p = 0.04) and **c)** abundance of foliage foraging spiders collected from plants only in 2003 (No significant difference; p>0.05).

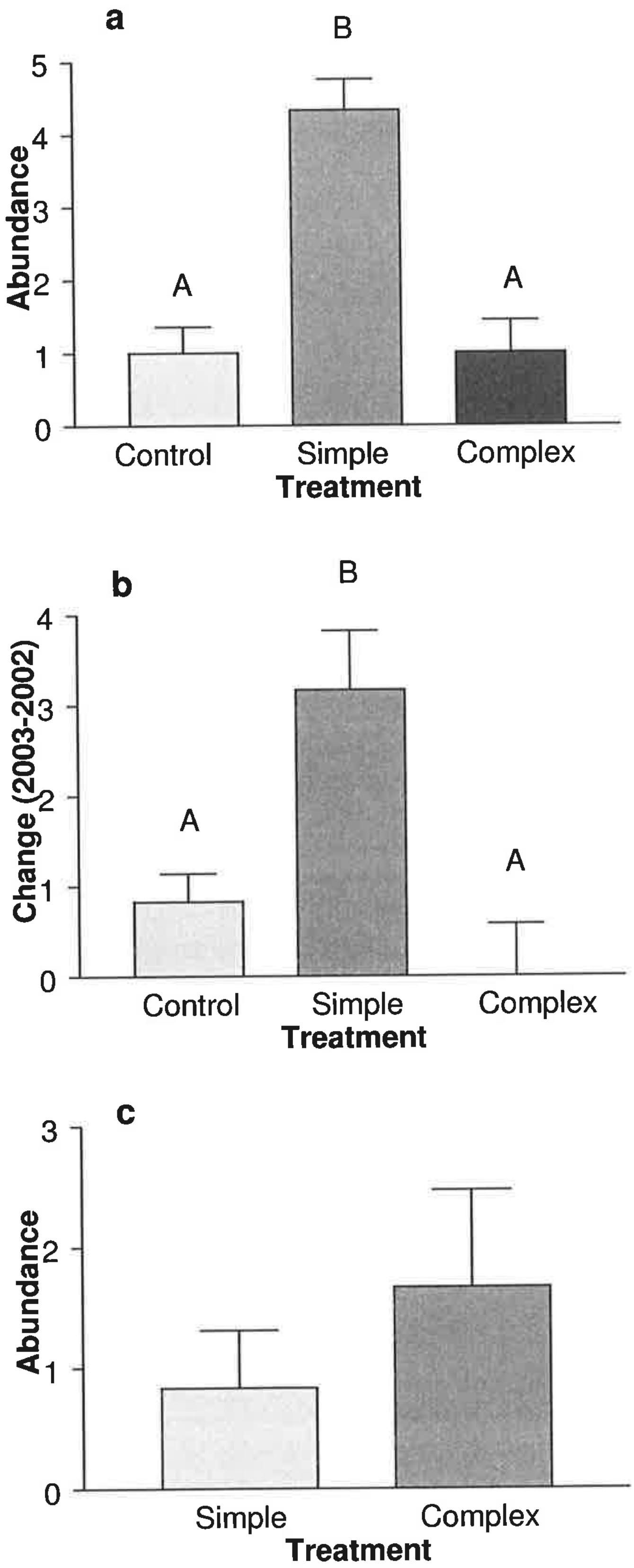


Figure 4.11 a) Abundance of spiders that forage both in foliage and on the ground collected in plots in 2003 (pitfall trap and plant samples combined) (χ^2 = 11.48, DF = 2, p = 0.0032), **b)** change in number of spiders that forage both in foliage and on the ground collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) (χ^2 = 9.94, DF = 2, p = 0.007) and **c)** abundance of spiders that forage both in foliage and on the ground collected from plants only in 2003 (No significant difference; p>0.05).

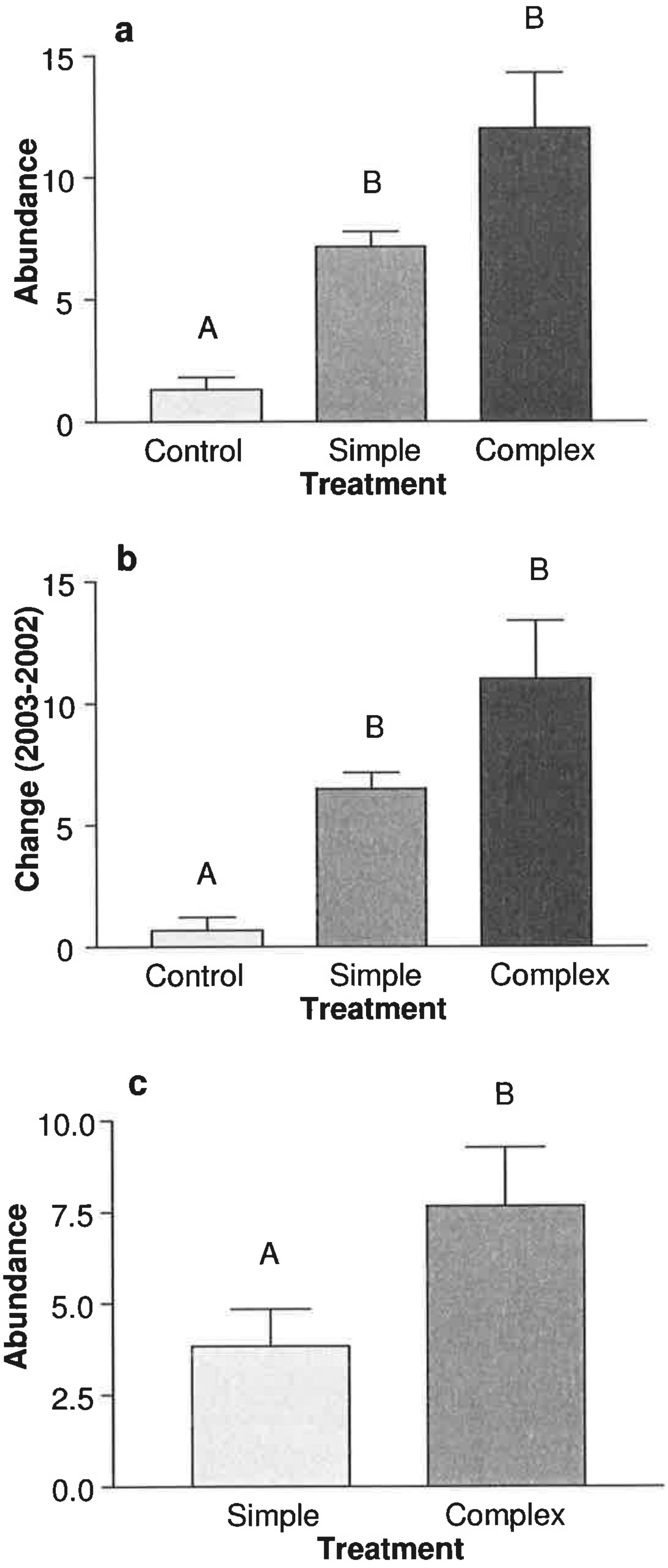


Figure 4.12 a) Abundance of ground foraging spiders collected in plots in 2003 (pitfall trap and plant samples combined) ($\chi^2 = 11.57$, DF = 2, $p = 0.003$), **b)** change in number of ground foraging spiders collected in plots between 2002 and 2003 (pitfall trap and plant samples combined) ($\chi^2 = 11.11$, DF = 2, $p = 0.0039$) and **c)** abundance of ground foraging spiders collected from plants only in 2003 ($\chi^2 = 5.41$, DF = 2, $p = 0.020$).

The ordination clearly shows the different spider communities associated with the three different treatments (Figure 4.13). The Araneidae, Corrinidae, Dictynidae, Gnaphosidae, and Zoridae all increased in numbers as the structural complexity in the plots increased, while Oxyopidae contributed to the position of the control plots in the bottom half of the ordination. The Multi-Response Permutation Procedure results revealed a significant difference among the treatment types based on the spider community composition (T = -7.527, A = 0.311, p = 0.0001).

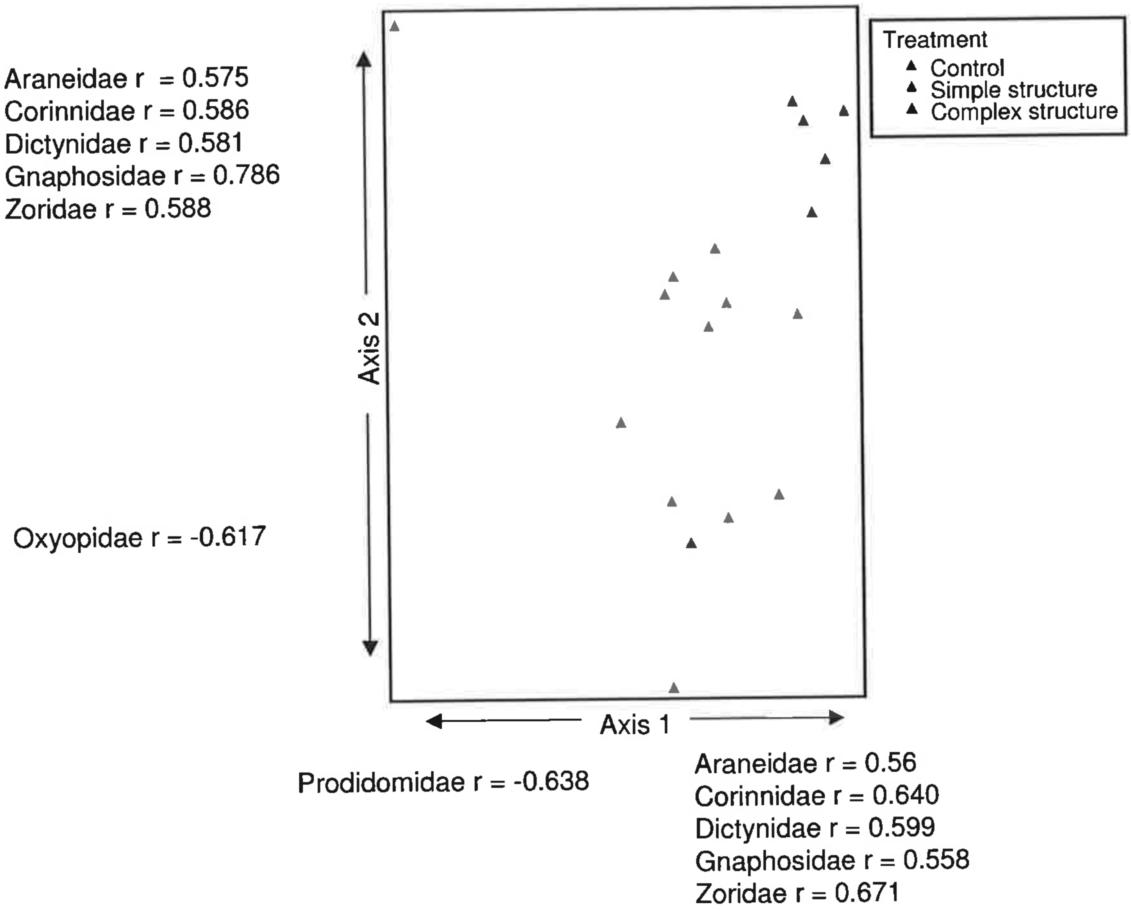


Figure 4.13 Two dimensional NMDS ordination of spider community composition within plots with simple, complex or no added structure, using family level abundance data (stress = 9.665, instability = 0.0023).

4.3.2 Ants

No significant response for any ant morphospecies, genus or functional group was detected when the change in abundance between 2002 and 2003 was analysed. When the 2003 data only were analysed, log (x+1) abundance of the Dominant Dolichoderinae and *Iridomyrmex* sp. B, revealed significant differences (Table 4.2, Figure 4.14). In this case the numbers collected in the plots with simple structure was significantly higher than in the control plots, whereas the complex plots were not significantly different from either (Figure 4.14).

Overall 74 species of ants, from 14 genera, were collected from the pitfall traps. There was no significant effect of treatment on the species richness of ants collected within the plots in 2003 but there was a significant block effect, with block 2 collecting more species than blocks 1 and 3 (Treatment F = 2.73, p = 0.10, Block F = 4.17, p = 0.040). There was no significant difference in the change in the ant species richness between the treatments between 2003-2002.

Table 4.2 Results of ANOVA of log (x + 1) number of ants from the Dominant Dolichoderinae functional group and of *Iridomyrmex* sp. B (*rufoniger* group).

Taxa	**Treatment**	**Mean**	**Tukey HSD**	**F Treatment**	**p Treatment**	**F Block**	**p Block**
Log Dom 03	0	2.18	A	5.07	0.024	3.68	0.054
	1	3.21	B				
	3	2.91	AB				
Log *I* sp. B	0	1.94	A	5.07	0.024	3.78	0.051
	1	3.21	B				
	3	3.91	AB				

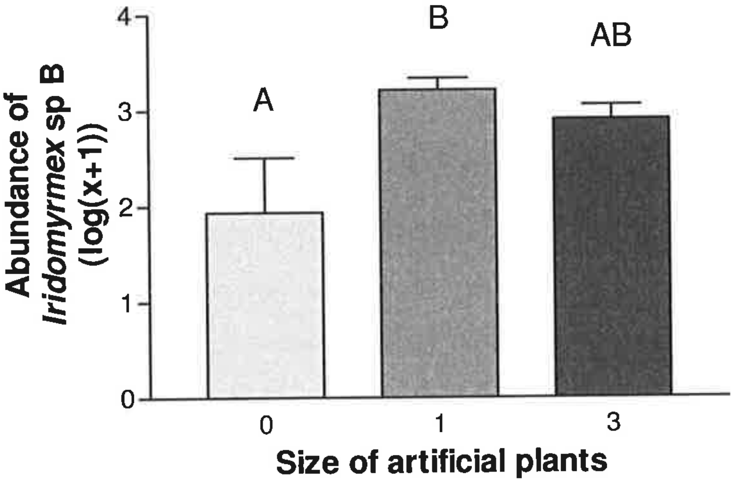


Figure 4.14 Number of *Iridomyrmex* sp. B (log x+1) (+/- SE) collected in plots with simple, complex or no plastic plants added, with Tukey-Kramer post-hoc test results above columns.

4.4 Discussion

An increase in structural complexity of the environment lead to the predicted increase in spider abundance, number of families and species richness but had little effect on the ant community. This appears to be a universal response among spider communities as it has been noted in a range of northern hemisphere environments including meadow (Greenstone 1984), shrub (Hatley and MacMahon 1980; Robinson 1981; Abraham 1983) and forest habitats (Rypstra 1986; Gunnarsson 1996; Halaj *et al.* 2000). Generally, when plant architecture was reduced, spider abundance and species richness decreased, while the opposite response occurred when habitat structure was increased. This phenomenon was evident in natural stands of different foliage density (Gunnarsson 1990), when foliage was removed or tied together (Hatley and MacMahon 1980; Scheidler 1990; Halaj *et al.* 2000), and under both field and laboratory conditions (Gunnarsson 1990). While these studies have reported similar responses of spider abundance and species richness to changes in habitat complexity in natural systems, the results of this experiment clearly demonstrate the particular importance of the abiotic component of habitat structure.

In the current study, while the number of artificial plants within a plot remained constant, the complex plants provided much greater structure and increased the abundance and species richness more so than for the simple structures. While other studies have increased habitat structure in an area by altering the number of structures (e.g. Rypstra 1983) or adding a single artificial structure of varying complexity (e.g. Robinson 1981), this study demonstrates that structural complexity can be more important for spider communities than the abundance of structures. It could therefore be presumed that spiders are strongly limited by the structural complexity of the environment, probably via a limited opportunity for recruitment. This suggests that in the vicinity of these plots there is a 'surplus' of spiders, probably mostly juveniles, able to colonise any suitable new patches. Addition of even greater structural complexity over a wider area may therefore have increased this effect even further, to a threshold where all of the species able to utilise and access the habitat were present. Food resources may then become a limiting factor. Many studies have demonstrated the importance of overall structural complexity of an area for spiders (e.g. Hatley and MacMahon 1980; Rypstra 1986); however, the interaction between the abundance of structures and complexity of a habitat remains relatively unexplored.

Most functional groups among the spider community responded positively to an increase in structural complexity, but the mechanism of colonisation of the structures and the reasons why they found them attractive probably varies among groups. One method employed by spiders to colonise new areas is ballooning (Mrzljak and Wiegleb 2000); using trails of silk to move through the air in a direction determined by the wind until snagged by a structure (Turnbull 1973). This is most common in juveniles, as a very light body weight is needed. Although the numbers of juveniles collected in each treatment plot were not analysed separately in the current study, a large proportion of spiders collected from the pitfall traps and plants were immatures. Abraham (1983) found that the number of spiders per shrub was also correlated with the size of the shrub and that many of the spiders in the bigger shrubs were immature (95%), suggesting that greater structure can collect more ballooning juveniles searching for new habitat.

Adult web-building spiders were also found on the artificial structures but in much lower numbers than juveniles. They tend to be much less mobile but can use aerial bridges of silk to move between plants and can climb over branches and foliage (Turnbull 1973). It is likely that the relatively thin and fragile structure provided by *Carrichtera annua* and other plants in the herbland is unable to support larger species and their webs, and surveys of the wider area are therefore needed to determine the source populations for these spiders. Sparse *Acacia victoriae* shrubs were present in the area and larger weed species in the nearby drainage lines. Supposing these were the source areas, some web-building spiders must have traversed considerable distances of up to 100 m to reach the artificial plants. In contrast, the coverage of such distances by active hunting spiders to reach the artificial structures is not unusual as they are adept at walking and climbing (reviewed in Turnbull 1973).

Just as the spiders must have employed a variety of dispersal mechanisms to reach the artificial plants, the reasons why they might have found the habitat suitable are also likely to differ among spider guilds. The increase in web-building species associated with an increase in habitat complexity is most likely due to their use of the structure to support their webs (Turnbull 1973; Greenstone 1984), which is otherwise limited in this ephemeral herbland. The decrease in abundance of web building species between 2002 and 2003 in the control plots may also be due to these spiders moving out of the control areas to the plots with extra structure. Small web-building spiders of the family Therididae were already present in the herblands before the experimental manipulations were set up, but many more web building species were present after the addition of structure, and this included many larger species. Gunnarsson (1990) also found an increase in spider size as structural density increased, although the reverse was observed in a subsequent study and, although the exact causes were unknown, it was suggested that interactions between structure, predation and competition may be important (Gunnarsson 1996).

Spiders known to actively hunt in foliage were also more numerous in the artificial structures and were probably attracted to the prey hunting conditions provided by the plastic plants. The large numbers of chiefly ground foraging spiders in the plants was more unexpected but has been noted previously (Halaj et al 2000, Hatley and MacMahon 1980). An overlap of different foraging groups in different structural layers is not unusual. Although a group of spiders may have a preference for a particular strata within the vegetation, in reality web builders and active hunters may be found in all structural layers depending on the time of the day or season (Abraham 1983; Morris 2000). For example, ground hunters may occasionally use taller vegetation as a vantage point and to escape from their own predators or the heat of the soil surface (Hatley and MacMahon 1980; Halaj *et al.* 2000; Morris 2000).

The artificial structures are likely to offer the spiders a more favourable microclimate in summer than the ground and ephemeral plants alone. The temperature just above ground level is likely to have been a number of degrees cooler (reviewed in Cloudsley-Thompson 1962) and the dense 'foliage' of the plastic structures would have provided more shade than is available on or under *Carrichtera annua*. The slight decrease in abundance of spiders in pitfall traps noted in the plots offering the most complex structure compared to the control areas suggests that spiders previously foraging on the ground or low herbs had moved into the canopy. An effect of climatic variables on spiders is also suggested by the increase in total abundance in collections from both treatment and control plots between the two years. The increase in numbers is likely to be the result of greater activity of spiders due to the higher temperatures experienced in the second season (Cloudsley-Thompson 1962; Rypstra 1986). These results agree with hypotheses suggesting that a substrate for foraging and an optimal microclimate are important determinants of spider distributions (Abraham 1983).

The division of spiders into families offers little additional information to explain differences in community composition between the three types of plots. Once again, there was a mix of all foraging types within each plot. The families with greater numbers in the complex plots consisted of two web-building families (Araneidae and Dictynidae), an ambush ground hunter (Corinnidae) and an active ground hunter family (Zoridae). Those with greater numbers in the less structurally complex plots contained active hunting families (Clubionidae and Salticidae) and web-building families (Theriidae and Zodariidae).

Salticidae, Araneidae and Theridiidae were likewise shown to increase with the cover of perennial grasses in the Northern Territory but, whereas the abundance of Zoridae correlated with the amount of bare ground (Churchill and Ludwig 2004), in this study they were found in greater numbers in the plots with the greatest structural diversity. Most Araneidae are orb weavers and they undoubtedly need access to more complex vertical structures to support their large webs.

Even though the spider community appears to be strongly linked to the plant community through the vegetation architecture, prey abundance, which may or may not be affected by canopy structure, is also likely to influence habitat suitability (Gibson *et al.* 1992; Halaj *et al.* 1998). However, no increase in potential prey species was observed (apart from other spiders), and there are two possible explanations for this; 1) the abundance of prey may not increase, or 2) prey may increase but are eaten by the greater number of spiders. The increase in structure may also reduce cannibalism and intra-guild predation by providing spiders with a place to hide before they make their webs (Rypstra 1983).

It is difficult to tease apart the relative importance of structure and prey availability as they may be intimately linked (Halaj *et al.* 1998). While McNett and Rypstra (2000) found structure and not prey availability to be the best determinant of spider abundance, the activity of web building spiders has been equally linked to vegetation structure, microclimate and prey abundance (Rypstra 1986). Trials in which prey were also increased resulted in a higher density of spiders than those in which structure alone was increased (Rypstra 1983). Cannibalism and intra-guild predation can have large impacts on population dynamics (Polis 1981) and, while they can be a ‘lifeboat’ mechanism for populations to survive times of low prey availability (Claessen *et al.* 2003), if other prey do not become available on artificial structures or cannot be sourced from elsewhere, this may reduce the long-term suitability of the habitat. The mechanisms that affect juveniles and adults are likely to be different, and hence further studies manipulating resource availability jointly with structural complexity that measure the fate of coloniser individuals are required. The current study also did not take into account the impact of vertebrate predators on spiders, such as birds and lizards, the abundance of which may also be linked to vegetation structural complexity (Gunnarsson 1996).

The results of this study suggest that a modest increase in structural complexity such as the restoration of the shrub overstorey to an ephemeral herbland would supply suitable habitat for spiders and increase spider abundance and diversity. However, the sensitivity of spider communities to habitat change on a large scale is currently unclear. Differences in spider assemblages were noted in grazed savanna and grassland habitats at increasing distances from stock watering points (Churchill and Ludwig 2004), while decreases in spider diversity but an increase in abundance were associated with increases in productivity due to urbanization within and around a city in the Sonoran desert (Shochat *et al.* 2004). However, no effect of grazing on spider communities was noted on a broad scale in eucalypt forests in New South Wales despite a reduction in the understorey habitat complexity, although a response to differences in cover and vegetation patchiness was noted on a local scale (Harris *et al.* 2003).

While the presence of artificial structures had a marked effect on the spider community, it appears to be of little consequence to the ant community. The effect of shading by the extra structure, although not measured, is likely to be small, since the more complex structures covered no more than 6% of the surface of the plots. The maximum shade level provided by the structurally complex plastic plants or the size of the plots in relation to the foraging range of many species may not have been great enough to elicit a response. However, *Iridomyrmex* sp. B was more abundant in plots with simple structures than in those with more complex ones, a response for which no explanation can be found.

The lack of a positive response to an increase in structure among the ant community is not particularly surprising since it does not include any resource augmentation, and may even increase predation pressure as a result of the greater numbers of spiders. Whereas ants generally build their nests on the ground in this semi-arid environment (Briese and Macauley 1977) and use shrubs and trees mainly to forage for nectar, and occasionally for microclimatic effects (Marsh 1985; Christian and Morton 1992), spiders use it to build webs and collect aerial invertebrates, as a vantage point for observing prey (Marc *et al.* 1999) and as a favourable microclimate (Abraham 1983). Other aspects of restoration of natural shrubland such as increased food resources, and greater increases in shade are, however, likely to have a positive effect on the ant community.

In conclusion, spiders clearly respond positively to an increase in structural complexity, with the complexity appearing to be more important than the abundance of structures in this semi-arid environment. In contrast, no response was noted among the ant community. Structure appears to be a limiting factor for spider communities, probably much more so than for other components of the fauna. To increase our understanding of the complex relationships between habitat structure and spider communities a number of subsequent studies are required. These include the independent manipulation of structural complexity and the number and distribution of artificial plants, as well as habitat structural complexity and food resources. Observations of longer-term succession of the spider community within the artificial plants would also be of interest, as many of the spiders collected may have been transient, including juveniles ballooning in, but to achieve this, the community should preferably be sampled without removal.

CHAPTER 5: ANT COMMUNITY RESPONSES TO INCREASED SHADE IN A SEMI-ARID HABITAT

5.1 Introduction

Vegetation is a primary determinant of ant community structure within any climatic zone (Andersen 1995). Variation in ant community composition is mainly due to abiotic factors associated with vegetation structure such as the shade produced by the vegetation altering the microclimate of the ants' environment (Andersen 1995) and the provision of structure on which to climb and escape from the heat of the ground surface (Christian and Morton 1992). However, biotic factors such as the carbohydrates available to ants from certain trees and shrubs (Davidson 1997; Blüthgen *et al.* 2000; Andersen 2003) also play a part.

At a biogeographic scale, shade appears to be the primary abiotic factor influencing ant community composition (Andersen 1995). On a local scale, the availability of shade is also likely to be important as ants have a relatively small body size and are not able to thermoregulate to any great extent (Marsh 1985). Any alteration in microclimate of their environment is therefore likely to have large effects on a wide range of species. While low temperature is a significant stress to the majority of ant species, high temperature can also be a stress but can often be avoided through changes in activity patterns that restrict foraging to the cooler parts of the day (Briese and Macauley 1980; Andersen 1995).

The relative importance of the shading effect of habitat structure is likely to differ among species. Species of *Melophorus*, for example, through physiological and behavioural adaptations are able to forage at extreme temperatures (e.g. well over 50°C surface temperatures) that are otherwise lethal to other species (Christian and Morton 1992). However, some ants such as the seed harvesting species within the genus *Pheidole*, are only able to forage at cooler temperatures (Briese and Macauley 1980; Morton and Davidson 1988).

The importance of shade at a biogeographic scale (Andersen 1995) and the partitioning of resource use through time within ant communities have been previously demonstrated (Briese and Macauley 1980), but local partitioning may also occur spatially in relation to microclimatic differences associated with shade. This chapter investigates the influence of shade on the foraging patterns of existing ant colonies within an open semi-arid environment. Previous manipulative studies have indicated the importance of shade to ant communities in forested areas (Smallwood 1982; Perfecto and Vandermeer 1996), where colony and forager activity were lessened in shaded areas. However, the opposite could be predicted in an open semi-arid habitat with very little perennial vegetation, where species are likely to be limited by high rather than low temperatures. As far as known, this is the first study to experimentally determine the importance of shade on the foraging patterns of ants within a semi-arid environment.

To assess the importance of shade to this semi-arid ant community, this factor was varied within small plots in an area devoid of perennial shrubs for several decades, but within close proximity to a remnant patch of shrubland. The *a priori* prediction was that variation in shade levels would affect the foraging activity of the various ant species (Briese and Macauley 1980) and overall community structure. This could be brought about through species choosing to forage elsewhere, as well as the migration of nest sites (Carlson and Gentry 1973; Smallwood 1982; Smith *et al.* 1987), and subsequent variation in interspecific competition (Perfecto and Vandermeer 1996). However, the short time frame of five months over which this experiment was undertaken limits this study to the impact of shade cover on foraging activity of existing colonies only.

The specific questions this study aimed to answer are; do the foraging patterns of members of the ant community within this environment respond to the addition of shade? If so, which groups are most responsive, and what is the optimum shade level for these groups?

5.2 Methods

5.2.1 Study site

The experiment was conducted in an ephemeral herbland, dominated by the exotic annual *Carrichtera annua* (Wards weed) near Oraparinna in the Flinders Ranges National Park (31° 17.24'S, 138° 50.44'E) in South Australia. This area once supported chenopod shrublands (Symon 1971), dominated by low bluebush (*Maireana astrotricha*, Chenopodiaceae). Within the semi-arid regions of South Australia many areas of chenopod shrubland are severely degraded as a result of long term overgrazing by sheep. At its most severe, this degradation has resulted in the total loss of all perennial chenopod shrubs, leaving an ephemeral herbland dominated by exotic annual weeds and a sparse scattering of *Acacia victoriae* shrubs. Even after the removal of stock, the recovery of the perennial shrubland is hampered by the slow rate of recovery in arid and semi-arid ecosystems (Westoby *et al.* 1989) and by a paucity of viable seed in the soil seed bank (Meissner and Facelli 1999; Hunt 2000). The removal of perennial shrubs reduces the total shade cover from approximately 20% to zero.

Three blocks, each consisting of 16 plots in a 4 x 4 square, were established within the ephemeral herbland (Figure 5.1). Each plot was 5 x 5 m and separated from the next by 25 m, making each block 95 m on each side (Figure 5.2). Approximately 200 m separated Block 1 from Block 2 and 100 m separated Block 2 and 3. The difference in separation of the blocks was necessary to ensure that individual ant colonies were unlikely to forage in more than one block and that enough flat, relatively undisturbed ground was available for each block. Ten plots in each block were randomly chosen for this experiment making a total of 30 plots (Appendix 5). The remaining 18 plots within the three blocks were used for the addition of artificial structure experiment (Chapter 4). The 25 m between each plot was thought to be sufficient to minimise interference between the two manipulations.

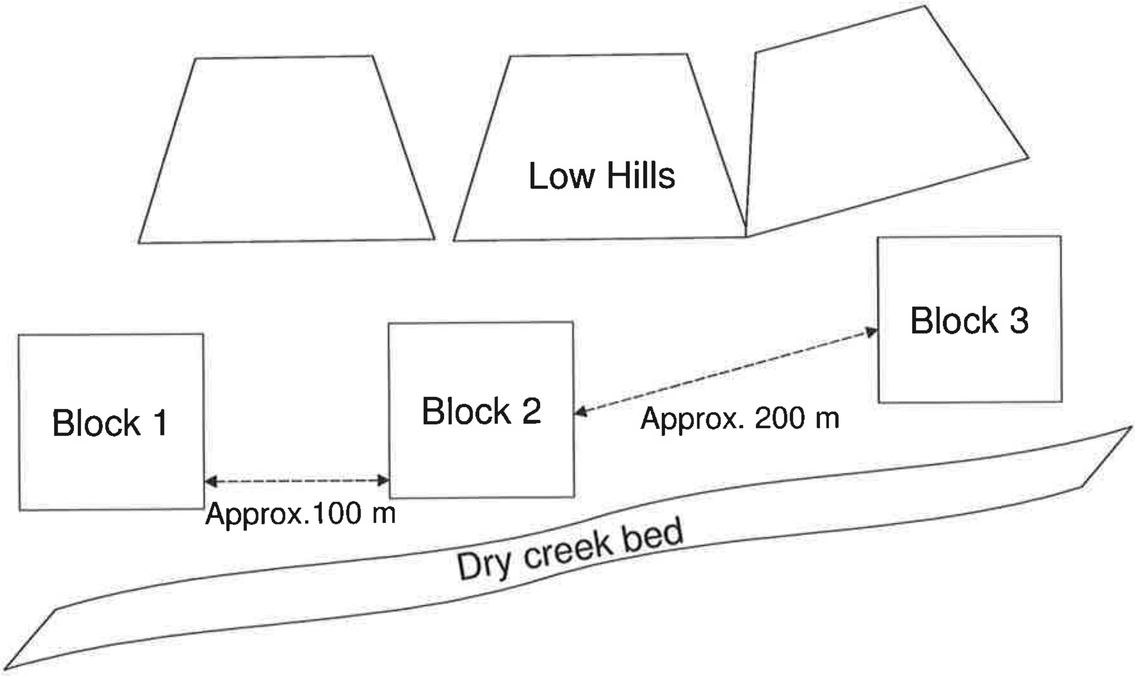


Figure 5.1 Arrangement of experimental blocks within the ephemeral herbland site. Not drawn to scale.

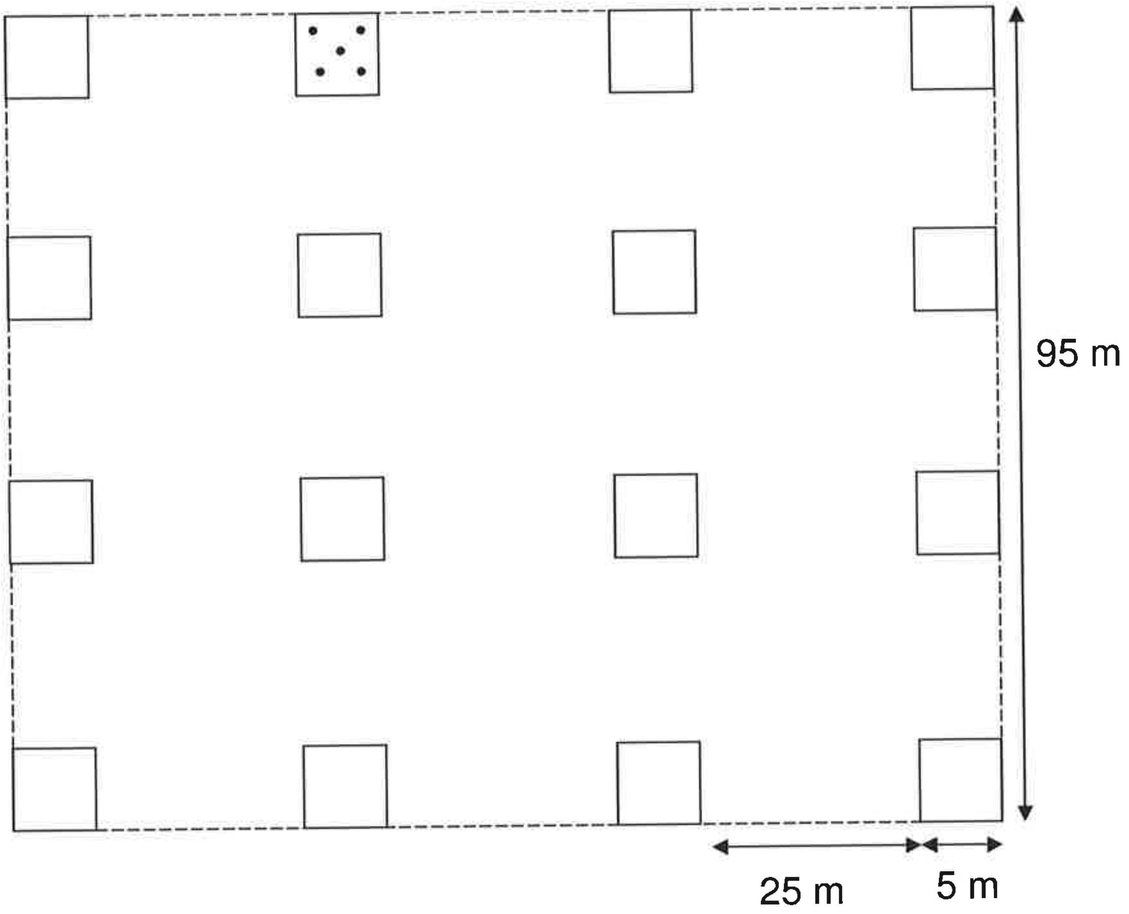


Figure 5.2 Plot and pitfall trap layout within experimental blocks. Small squares represent plots and black circles pitfall trap locations.

5.2.2 Experimental design

Normal shade levels in nearby low bluebush shrubland, measured in a series of 5 x 5 m plots, is approximately 20% so shade levels were artificially increased to between 5 and 50% cover to represent all conditions that the ants are likely to encounter within a shrubland. Access to available food resources was unchanged.

Shade was manipulated using shade cloth tents made of black 70% shadecloth (SARLON) (70% of light is blocked) of 60 x 60 cm size stapled to four 45cm wooden stakes, which were hammered into the ground until standing 25 cm high. A 5 cm overhang was left on each edge so that the final size of the top of the shade tent was 50 x 50 cm. This approximated the diameter, height and shading provided by a low bluebush (*M. astrotricha*).

Plots were randomly assigned a percent cover of the total area (one tent producing 1% cover) up to 50% at 5% intervals. Thus a plot with 10% cover had 10 tents and a plot with 50% cover had 50. The small increments in shade cover were designed to encompass the preferred foraging environment for all species as well as variation in activity levels across a range of shade levels for each species. Each block contained plots with a range of shade levels and the total number of plots receiving a particular shade level across all blocks varied between 2 and 4. The tents were randomly assigned to positions on a 10 x 10 grid within each plot using only alternate squares (see Appendix 6 for arrangement of tents within plots). Because of the disturbance associated with the placement of tents, all plots, including the 0% cover plots, were equivalently trampled during the installation process.

The shade tents were erected in July 2003, and ants were sampled using pitfall traps for a 48 h period in December 2002 (pre-treatment baseline data) and again in December 2003 (five months following treatment). Each 5 x 5 m plot contained five pitfall traps in a star design, one in the middle and four radiating to the corners of the plot, 2.5 m from the centre. Each pitfall trap consisted of a 68 mm diameter plastic specimen jars in 75 mm PVC pipe. Approximately 50 mL of 50% ethylene glycol (1.5 cm depth) was added to each jar along with a couple of drops of detergent to break the surface tension. The weather during the 2002 sampling period was warm and windy (Day 1 25℃ (windy), Day 2 25℃ (windy), Day 3 27℃ (no wind)). During the 2003 sampling period the weather was hot with a cooler change and light showers on the final day (Day 1 32℃ (overcast), Day 2 41℃ (mostly sunny), Day 3 20℃ (light showers in morning, fine but cloudy in afternoon)).

After collection, specimens were then transferred to 70% ethanol. Ants were sorted to species and assigned to a functional group according to Andersen (1995). Ant voucher specimens have been lodged in the Waite Insect and Nematode Collection, Waite Campus, The University of Adelaide.

5.2.3 Analysis

Data were pooled across all blocks for each shade level for analyses to ensure an adequate sample size. To account for seasonally related variation in the ant community, the composition at species and functional group levels were compared between the two years, 2002 and 2003.

To compare differences in community composition among shade levels, the 2003 post manipulation log (x + 1) abundance data for all species collected in each plot were analysed by Non-metric Multidimensional Scaling (NMDS) (Euclidean Distance measure) using PC-ORD 4.10 (McCune and Mefford 1999). Each plot was classed by shade level; low (0-10% shade cover), medium (15-30%) or high (35-50%). Multi-Response Permutation Procedures (MRPP), a non-parametric multivariate test for detecting significant differences between groups (McCune and Grace 2002) was used to test for significance of separation of the low, medium and high shade level plots and each shade cover level. The Euclidean distance measure was used.

The abundance of common ant species, genera and functional groups collected in December 2003 were each analysed in relation to shade cover using regression analysis. The data displayed very high variation within each shade cover level, resulting in an envelope effect (Goldberg and Scheiner 1993). This arises when many factors, aside from the one being manipulated, produce variation among the data. A maximum response may be produced by the variable under investigation but the variation underneath may be caused by other factors (Goldberg and Scheiner 1993) that, in this case, could be several variables including the proximity of a nest to the plot. The level of variation was not constant across the values of the independent variable, leading to a violation of the statistical assumption of homoscedasticity necessary for regressions. Transformations did not succeed in producing linearity nor did they improve r^2 values. Quantile regressions are the most appropriate statistical technique to use for data displaying this type of response (Cade *et al.* 1999; Huston 2002; Cade and Noon 2003). However, the sample size used in this study was not large enough to employ this method. Instead, for each common species, genus and functional group, linear and non-linear regression analyses (Gaussian curves provided the best fit for most analyses using the untransformed data) of ant abundance against shade level were performed on; 1) the full data set, 2) the highest abundances found within the plots for each of the 11 shade levels, and 3) the 75th quartile of the pooled data for shade levels (0-5, 10-15, 20-25, 30-35 and 40-50%) (n=5). Linear and non-linear regressions were fitted using PRISM Graphpad (Version 3.03). As it is difficult to apply significance tests to non-linear regressions these were not performed.

5.3 Results

5.3.1 Ant community composition of site

A total of 53 ant species, belonging to 12 genera were collected within the three blocks over the two years. *Iridomyrmex* and *Melophorus* were the most speciose genera, each with six species represented. The overall makeup of the ant community did not appear to change substantially between the two years. Dominant

Dolichoderinae ants were the most abundant in both years although much more so after the manipulations. In both years, the high numbers were largely due to one abundant and widespread species, *Iridomyrmex* sp. B (Figure 5.3, Appendix 7). The log transformed data diminished the bias of this abundant group and revealed the other functional groups present in the community more clearly. The next largest group of ants belonged to the Generalised Myrmicinae and Hot Climate Specialists, while generally lower numbers of Opportunists and Specialist Predators were collected (Figure 5.3, Appendix 7). *Melophorus* sp. U was the most abundant Hot Climate Specialist species, and, of the Generalised Myrmicinae, *Pheidole* sp. B and H and *Monomorium* sp. L were collected in high numbers but not in all plots (Appendix 7). The relative abundances of these species were similar in both years. One difference between the two years was the presence of low numbers of two *Stigmacros* spp. from the Cold Climate Specialist functional group in 2002 that were not collected in the subsequent year.

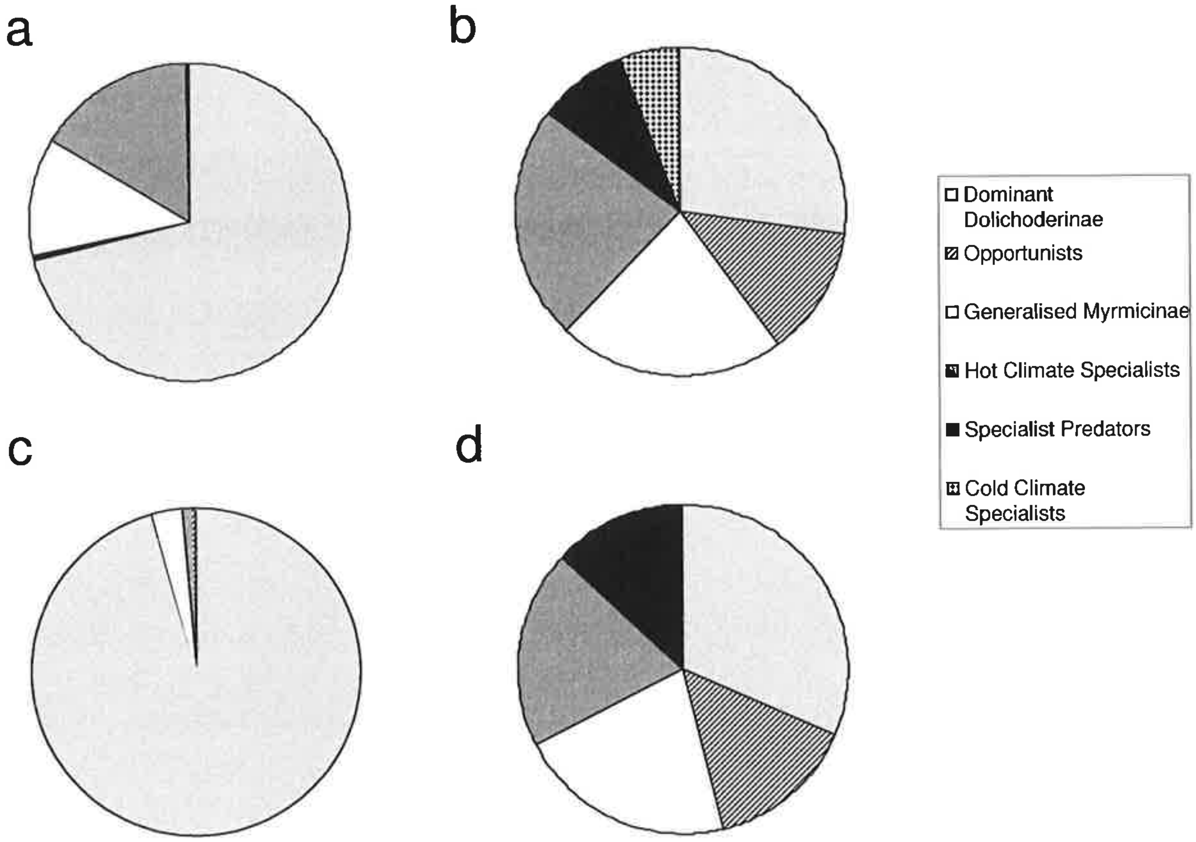


Figure 5.3 Functional group composition of all plots combined collected in pitfall traps in summer 2002 prior to shade manipulations, displayed as **a)** raw data and **b)** log (x+1) and in summer 2003 after shade addition, **c)** raw data and **d)** log (x+1).

5.3.2 Responses to shade

The collections from the following summer after shade had been added to the plots show no obvious grouping according to shade level in the multivariate analysis at either species or functional group levels (Figures 5.4 and 5.5). However, the MRPP results were significant for both species and functional group for grouping at low, medium and high shade levels but not for individual shade levels (Table 5.1).

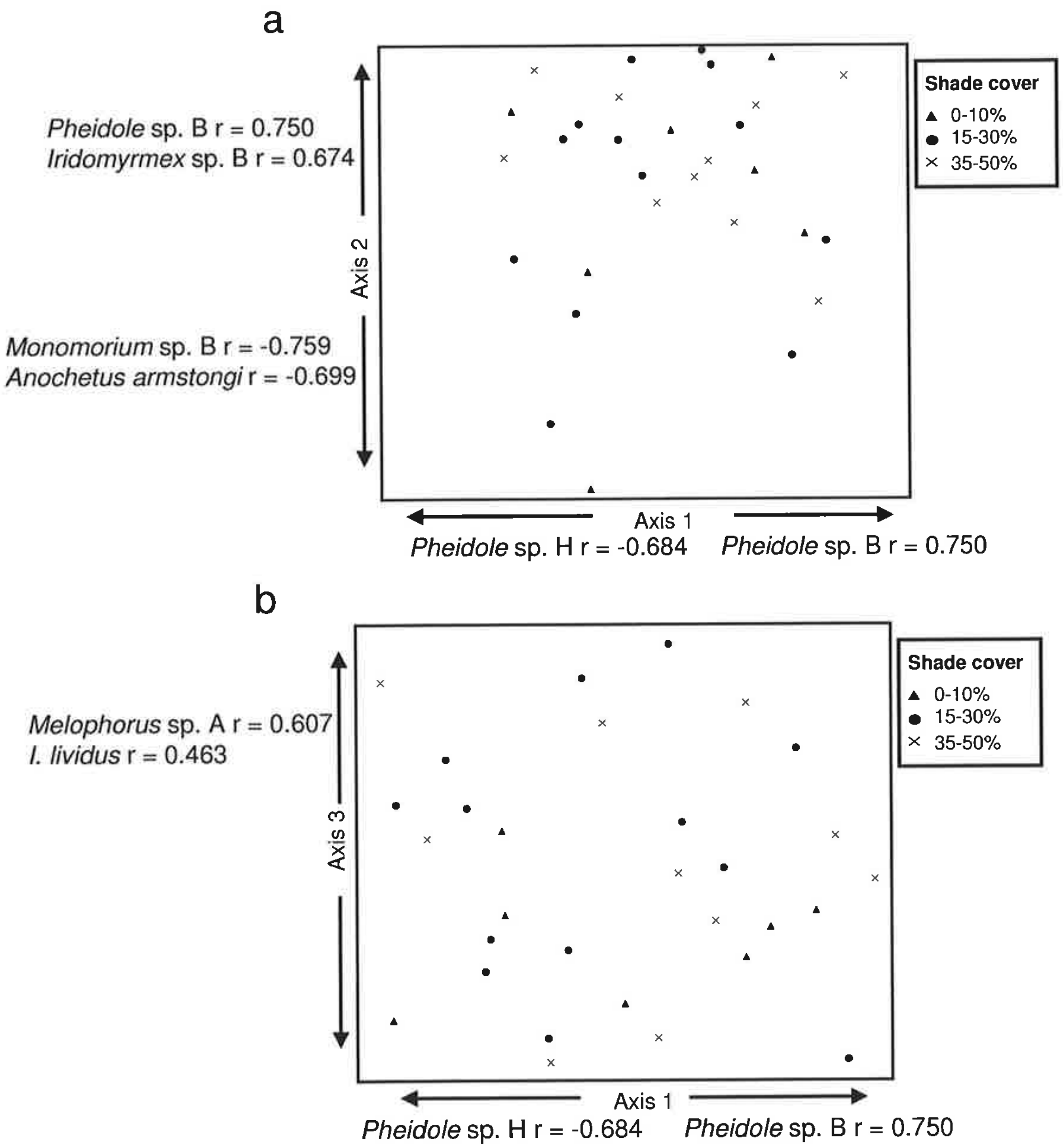


Figure 5.4 Three dimensional NMDS ordination of ant species abundances (log (χ +1)) 2003 data (stress = 13.94, instability = 0.004) **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Species with greatest correlation with axes are shown and direction of correlation indicated by arrows.

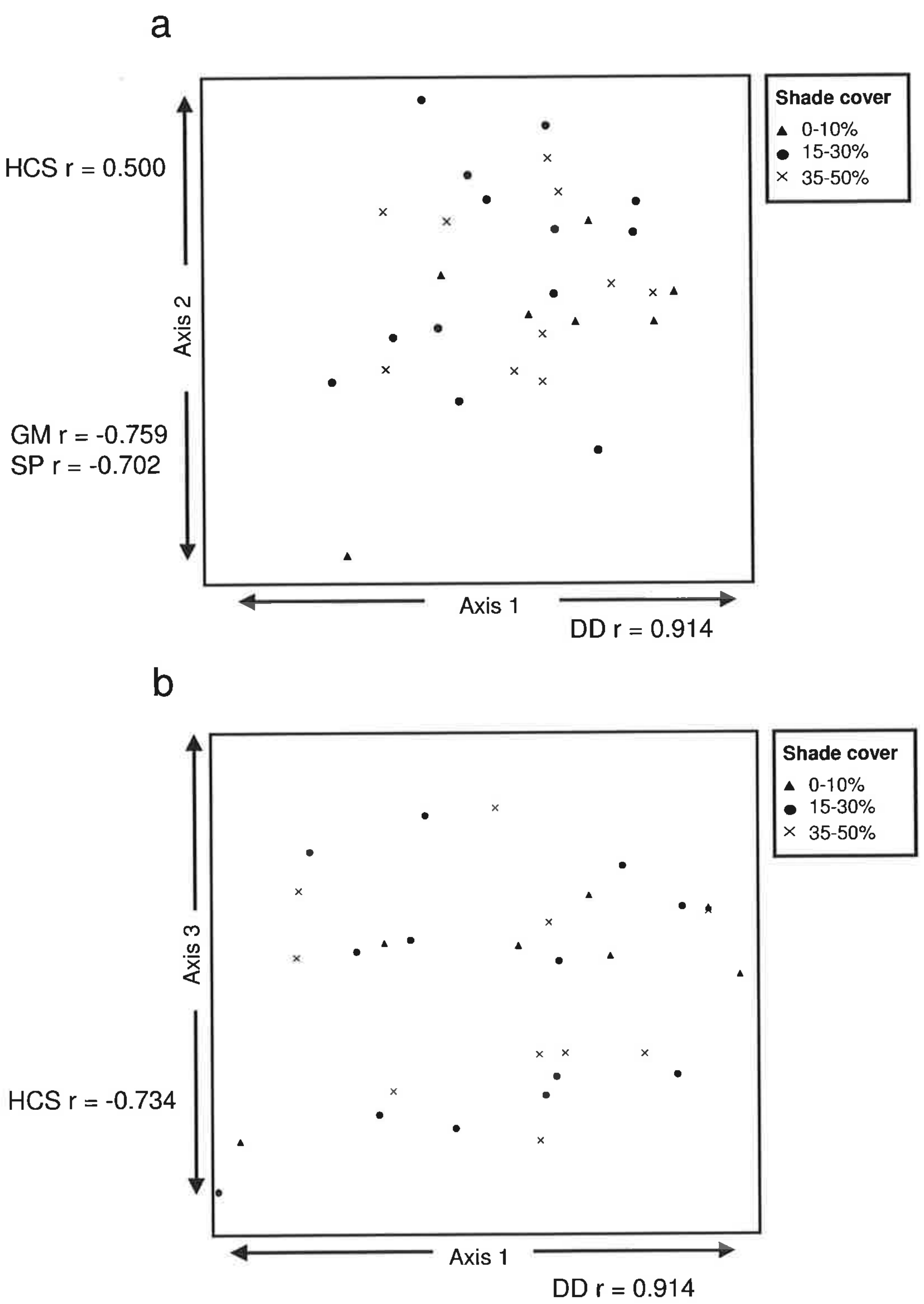


Figure 5.5 Three dimensional NMDS ordination of ant functional group abundances (log (χ +1)) 2003 data (stress = 11.45, instability = 0.004) **a)** Axes 1 and 2 and **b)** Axes 1 and 3. Functional groups with greatest correlation with axes are shown and direction of correlation indicated by arrows.

Table 5.1 Multiresponse Permutation Procedure results testing for significant grouping by shade cover level, including values for T (test statistic), A (agreement statistic) and a *p*-value.

	Year	Group	T	A	*p*
Species (log x+1)	2003	Low, med, high	-15.20	0.347	<0.001
	2003	Individual	-1.308	0.044	0.098
Functional Group (log x+1)	2003	Low, med, high	-15.11	0.44	<0.001
	2003	Individual	-1.66	0.093	0.054

Ten species (*Pheidole* sp. B, *Pheidole* sp. H, *Melophorus* sp. U (*fieldi* group), *Melophorus* sp. J (*wheeleri* group), *Melophorus* sp. D (*froggatti* group), *Iridomyrmex* sp. B (*rufoniger* group), *Rhytidoponera metallica*, *Anochetus armstrongi*, *Monomorium* sp. L (*sordidum* group), and *Tetramorium* sp. J (*impressum* group)), six genera (*Pheidole*, *Melophorus*, *Iridomyrmex*, *Rhytidoponera*, *Monomorium* and *Tetramorium*), and four functional groups (Dominant Dolchoderinae, Hot Climate Specialists, Opportunists, and Generalised Myrmicinae) were common enough for regression analysis. No significant linear regressions were found for any species or group (Appendix 8). However, a number of high r^2 values were obtained for non-linear regression analyses (Appendix 8). It was decided that these were only likely to be biologically significant if both the maximum and 75th quartile regressions had high r^2 values and similar patterns of response, and those that appeared to be disproportionately influenced by single values were disregarded.

The Hot Climate Specialist functional group showed a clear response after the addition of shade with a peak in activity at around 25% shade cover (Figure 5.6.). The genus *Melophorus* displayed the same response (Figure 5.7.), but this pattern was largely due to the response of a single species *Melophorus* sp. U (Group F) (Figure 5.8.), whose activity peaked at 30% shade cover. The other common *Melophorus* species, sp. J (*wheeleri* group), did not show any response to the addition of shade (data not shown). *Pheidole* spp. also responded to shade with a maximum activity around 20% cover (Figure 5.9.), while *Pheidole* sp. H displayed a peak at 15% (Figure 5.10).

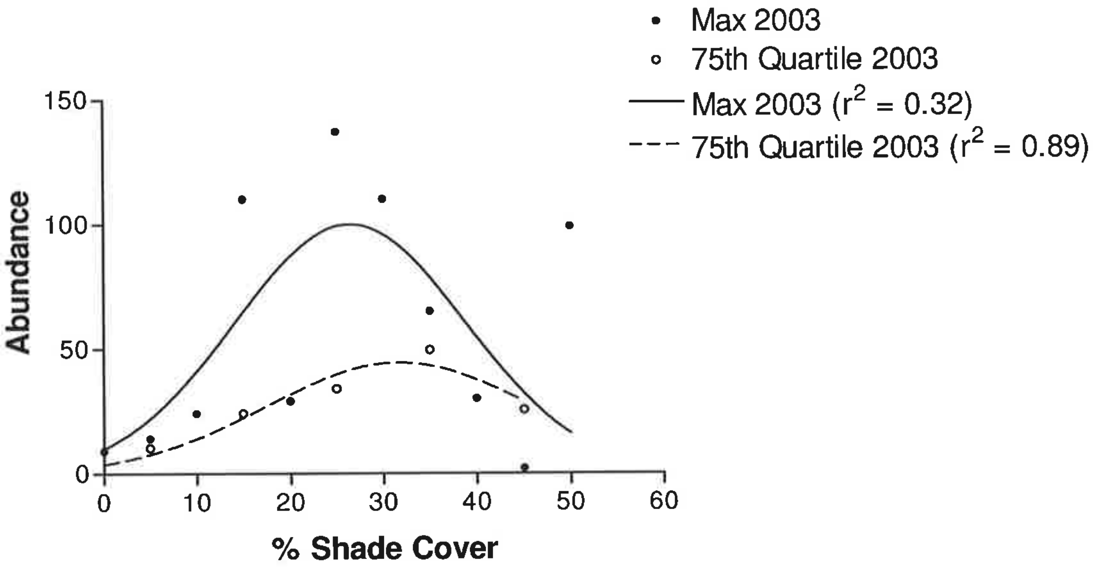


Figure 5.6 Total number of Hot Climate Specialist spp. collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are shown.

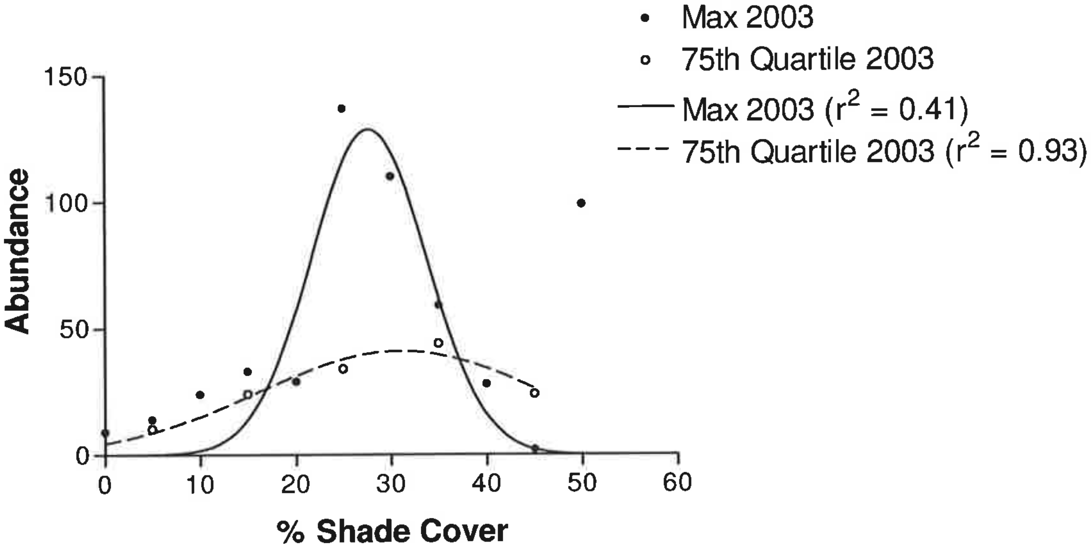


Figure 5.7 Total number of *Melophorus* spp. collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are shown.

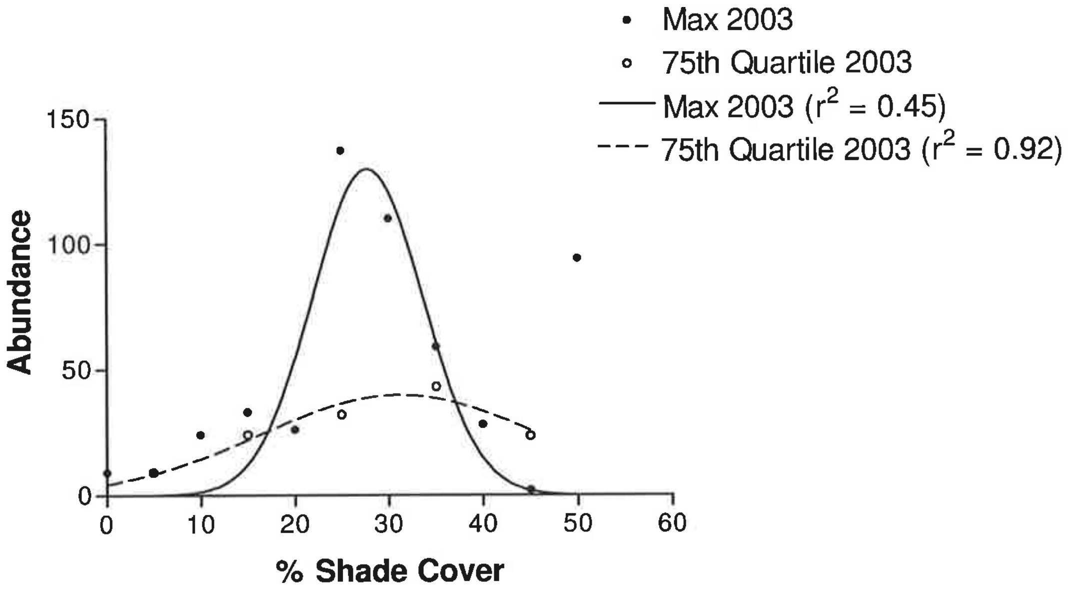


Figure 5.8 Total number of *Melophorus* sp. U (Group F) collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are shown.

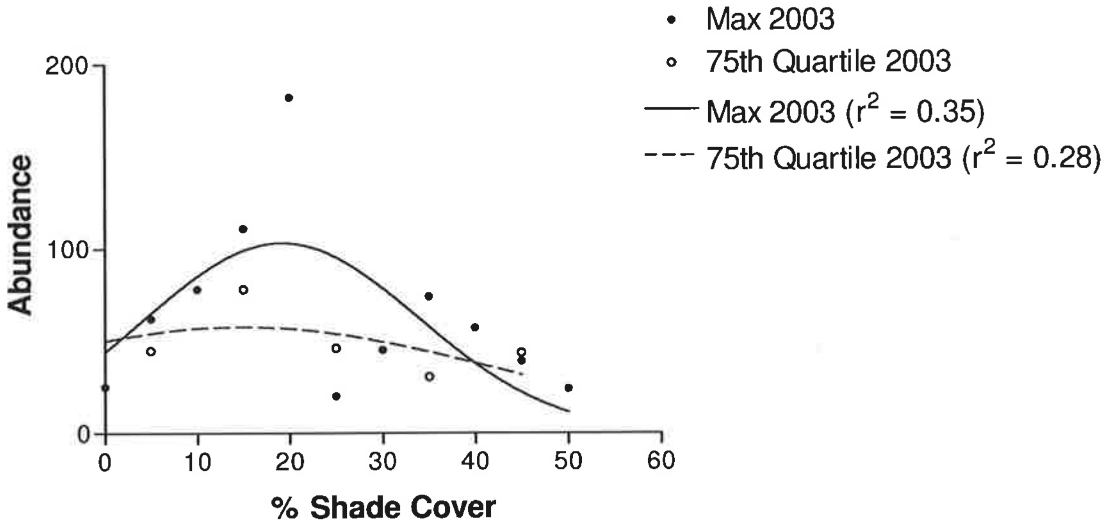


Figure 5.9 Total number of *Pheidole* spp. collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are shown.

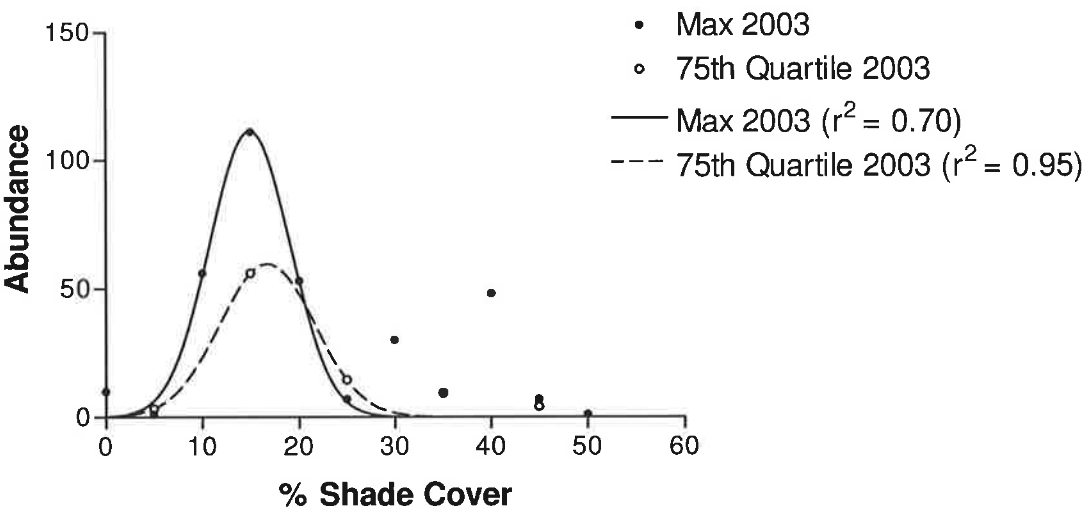


Figure 5.10 Total number of *Pheidole* sp. H collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are displayed.

The activity of *Tetramorium* spp., members of the Opportunist functional group, also peaked at about 15% shade cover (Figure 5.11). The highest abundance of individuals from the Specialist Predator functional group was at the lowest shade level. However, this was mostly due to a single large collection of the most common predatory species, *Anochetus armstrongi*, from one plot. None of the other functional groups, genera or species showed any pattern of response to the addition of shade.

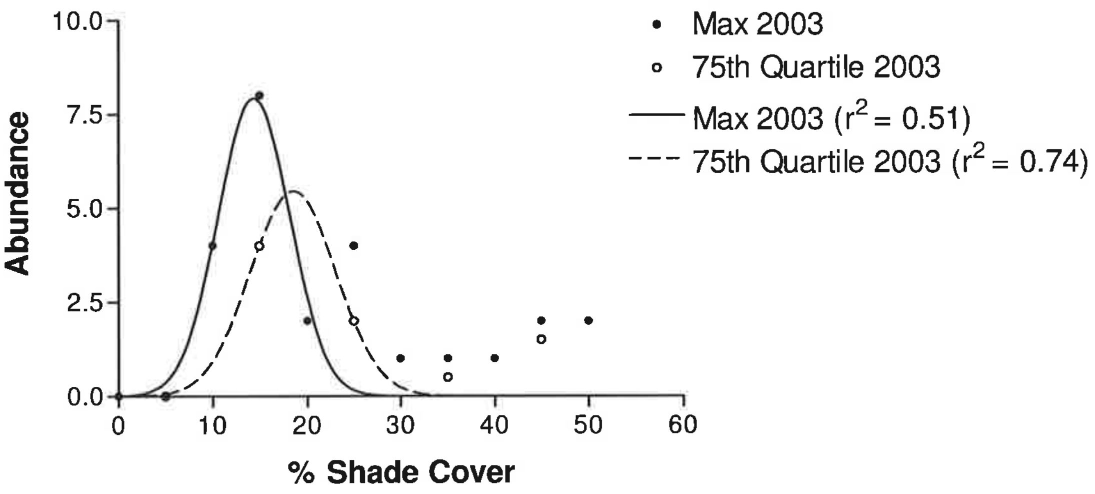


Figure 5.11 Total number of *Tetramorium* sp. collected in pitfall traps in plots with increasing shade cover. To improve clarity, data points and regression results (r^2) for maximum values and 75th quartiles from 2003 only are displayed.

5.4 Discussion

The overall ant community composition did not appear to be greatly influenced by the addition of shade. The majority of ant species, including the dominant *Iridomyrmex* species, did not exhibit a response to increased shade. This could mean that shade is not an important factor determining foraging activity in this ant community, at least at this time of year. It is possible that some of the less common species also altered their foraging activity in response to the increase in shade, but the low number of individuals collected meant any response could not be analysed and so was not detected.

The three taxa that did respond (*Pheidole*, *Tetramorium* and *Melophorus*) showed a positive increase in activity for intermediate shade levels, similar to that found in nearby chenopod shrubland. For *Melophorus*, this can be explained by the thermal refugia provided by the shade structures. This genus is known for its heat tolerance (Briese and Macauley 1980; Christian and Morton 1992; Hoffman 1998) and its ability to forage in the middle of summer days for arthropod prey that have succumbed to heat stress (Greenslade 1979; Morton and Davidson 1988). The heat tolerance is achieved through behavioural adaptations such as the use of thermal refugia, periodically seeking cooler conditions under shade or on vegetation (Marsh 1985; Christian and Morton 1992), that allow them to forage for longer periods at high temperatures (Marsh 1985).

As well as behavioural adaptations, many *Melophorus* species appear to have a physiological advantage over other ant species. One species has been observed to have a critical thermal maximum of 56.7°C and to be able to survive for 1 h at 54°C (Christian and Morton 1992). *Melophorus* is known to actively avoid foraging at cooler temperatures, suggesting the behaviour is directed to avoidance of competition with other species that have similar ecological requirements (Christian and Morton 1992). This may explain the negative response in the activity of *Melophorus* sp. U under high shade cover.

There is no evidence that *Pheidole* or *Tetramorium* species use shade as thermal refugia; they instead appear to have an optimum foraging temperature range that may have been equivalent to that found under intermediate shade cover. The optimum foraging range of *Pheidole* appears to be between 25-35°C, with some species also foraging nocturnally (Morton and Davidson 1988). This results in foraging being restricted to the cooler parts of the day (early morning and late afternoon) during summer, but high activity levels can be maintained throughout the middle of the day in spring (Briese and Macauley 1980). *Tetramorium* spp. also display a similar habit of foraging in the early morning and evening (Shattuck 1999), suggesting that they too have a relatively low optimal foraging temperature. Similar shade structures installed in a semi-arid environment reduced soil surface temperatures by 10-15℃ in the middle of the day (J. Facelli, unpublished data). The application of shade in this experiment is therefore likely to have lowered temperatures sufficiently to allow the *Pheidole* and *Tetramorium* ants to forage for longer periods during the day, thereby increasing the numbers caught in pitfall traps. An increase in the activity levels (Perfecto and Vandermeer 1996) and duration of surface activity (Smith *et al.* 1987) of *Pheidole* species has also been noted when shade cover was increased within a tropical non-monomorphic coffee plantation and a Sonoran Desert shrubland, respectively.

The larger foraging range of *Iridomyrmex* species may mean than many of the individuals collected in pitfall traps were following a foraging trail to another area rather than actively foraging within the 5 x 5 m plot, and this could explain the lack of any pattern of forager activity with the increase in shade cover. Foraging by *Iridomyrmex* sp. B, in particular, appears to be closely linked to the presence of *Acacia victoriae*, the only perennial shrubs remaining in degraded herblands in the Flinders Ranges, and the honeydew producing Homoptera (*Sextius* sp. (Membracidae)) that infest it. Although *Iridomyrmex* species have been observed to forage throughout the day in summer (Briese and Macauley 1980), the presence of honeydew as a food resource may override any microclimatic effect of shade. Spending a large amount of time on these shrubs rather than foraging on the ground means they will also experience lower temperatures than other species in the community that forage exclusively on the soil surface.

The lack of response among a large number of other ant species may be linked to the fact that many, including *Rhytidoponera* and *Monomorium* species, switch from diurnal to nocturnal foraging in hot summer weather (Briese and Macauley 1980; Andersen 1983), and so may not be affected by the availability of shade during the day. However, for most species that switch to nocturnal foraging, the timing and levels of activity are closely linked with soil surface temperature and humidity (Briese and Macauley 1980), and if the decrease in soil temperature produced by shade was great enough it should allow them to forage diurnally despite the hot weather. The pitfall traps in this study were open for a full 48 h, so no record of diurnal or nocturnal foraging is available, but their foraging activity does not appear to have increased overall. More information on the importance of shade to these species may be gained by repeating the trapping at a cooler time of year when diurnal activity is more prevalent.

While the majority of ant species may not have been affected by the shade directly, there was also an absence of any obvious indirect response despite significant changes in a number of relatively abundant species. Interspecific interactions have been shown to be an important determinant of ant community structure in semi-arid environments (e.g. Greenslade 1976; Briese and Macauley 1977) but these results suggest that the interactions between these species and others in this ant community are not strong. However, the situation may have been different had the competitively dominant *Iridomyrmex* species been affected by the shade increase.

Changes in the activity levels of a number of species were noted five months after the addition of shade and the reproductive response of species within this ant community to an increase in shade could also be measured by extending the time frame of the experiment. The small amount of information available on colony and nest movement and establishment for species present in such semi-arid habitats suggests that under normal conditions nest establishment occurs relatively infrequently (Briese and Macauley 1980). However, a reproductive effect resulting in nest relocation in response to changes in shade levels has been noted in ant species in oak-hickory forest (Smallwood 1982) and open old-fields (Carlson and Gentry 1973) in the northern hemisphere.

In this generally hot and bare environment where access to shade is a limiting resource and ant diversity and activity are nevertheless high, it appears that the majority of species are not limited by access to shade. Many species may have evolved to live without shade and other factors such as access to food resources may be of much greater importance. Although not ubiquitous, shade is obviously important to a suite of ant species within this semi-arid community during the summer months, with an intermediate shade level of around 25% being the most favoured for activity by members of three genera. Indirect effects of shade on interactions among species in the community appear negligible in this system, primarily due to the lack of response from the competitively dominant *Iridomyrmex* species. This group, especially *Iridomyrmex* sp. B, seems instead to be influenced by access to carbohydrates from Homoptera on acacia shrubs. Repeat sampling six and twelve months later, may also provide some insight into the influence of shade on foraging activity in cooler months and nest migration within this ant community.

CHAPTER 6: THE ASSOCIATION OF A DOMINANT ANT SPECIES WITH HOMOPTERAN HONEYDEW IN SEMI-ARID SOUTHERN AUSTRALIA

6.1 Introduction

In addition to the importance of abiotic factors associated with the vegetation such as shade and structure (Andersen 1995), biotic factors such as the provision of food sources can also impact on ant communities (e.g. Briese and Macauley 1981; Andersen 2003) In particular, access to carbohydrates from nectar supplied directly by a plant or honeydew from an insect feeding on the plant has been linked with ant productivity and community structure. This association has been noted in environments as different as tropical rainforests (Blüthgen *et al.* 2000), sub-tropical plantations (Samways 1990) and semi-arid shrublands (Nash *et al.* 2000).

Access to liquid carbohydrates and particularly homopteran honeydew has been associated with the large ant colony sizes in tropical (Blüthgen *et al.* 2000) and sub-tropical environments (Samways 1990). The provision of this resource by shrubs and trees and their associated Homoptera appears to be equally important to ant communities in semi-arid environments around the world (Nash and Whitford 2000; Andersen 2003).

A reduction in the availability of homopteran honeydew is thought to be one of the main causes of lower abundances of the dominant liquid-feeding ant (*Conomyrma insana*) after the removal of Mesquite shrubs in a Chihuahuan Desert grassland (Nash and Whitford 2000). The exceptionally high ant abundances found in the semi-arid environments of Australia have also been attributed to the availability of liquid carbohydrates (Andersen 2003). *Eucalyptus* (Greenslade 1971) and *Acacia* (Andersen 2003) plants appear to be the most important sources of carbohydrates in Australia.

In all of these environments, behaviourally dominant ant species tend to monopolise these carbohydrate resources (e.g. Blüthgen *et al.* 2000; Nash *et al.* 2000; Andersen 2003) with often only a single ant species found on each plant (Dansa and Rocha 1992). Where both nectar and honeydew are available the most dominant species will often access honeydew sources in preference to nectar, leaving this instead to less dominant species (Blüthgen *et al.* 2000). The fuelling of large colonies of dominant ants can obviously have impacts on other ant species within a community, and this has been noted within the rainforest canopy where the availability and type of carbohydrate was clearly linked with ant community composition (Blüthgen *et al.* 2000).

The aim of this study was to investigate the importance of homopteran honeydew from acacia plants as a resource for a dominant ant species and other taxa within the ant community in a semi-arid environment. In semi-arid Australia, *Iridomyrmex* species are the main foragers and dominant species on shrubs, due to their ability to digest liquid food and aggressive nature (Andersen 2003). They have a large influence over other ant species within the community through their high abundance and aggressive behaviour (Greenslade 1976; Greenslade and Greenslade 1984a; Andersen 1990). This is certainly the case with the large meat ants (*Iridomyrmex purpureus* species group) (Greenslade 1976; Andersen 1992; Andersen and Patel 1994); and evidence suggests that smaller *Iridomyrmex* species can usurp dominance from their larger congeners under certain conditions (Greenslade 1976; Fox *et al.* 1985). This can affect other members of the ant community as particular dominant species often have a different suite of species with which they co-exist (Room 1975), and this phenomenon has been noted for *Iridomyrmex* species (Greenslade 1976).

In degraded semi-arid ephemeral herblands of the Flinders Ranges the removal of homopteran honeydew from *Acacia victoriae* shrubs is dominated by a small ant from the *Iridomyrmex rufoniger* species group. These small species can forage over large distances, making use of multiple interconnecting nests, and produce large numbers of workers (Briese and Macauley 1977). The distribution and abundance of these ants appears to be patchy and this uneven distribution may be related to the availability of carbohydrates from acacia shrubs. *Acacia victoriae* is found in both chenopod shrubland and degraded ephemeral herbland (Symon 1971), but they appear to be more common and more often infested by homopterans in degraded, overgrazed areas (personal observation).

It has been previously noted that ants collecting nectar or honeydew from plants frequently position their nests at the base of plants from which they obtain these carbohydrates (Bentley 1976; New 1984; Cushman and Whitham 1991; Dansa and Rocha 1992). The *a priori* prediction of this short-term study was therefore that the nests of this *Iridomyrmex* species would be clustered around the base of shrubs supplying homopteran honeydew. The prevalence of nests of a dominant species around acacia shrubs may also affect the position of nests of other ant species within the community as a result of interspecific competition.

The questions addressed here were: do *Iridomyrmex* sp. B nests tend to be clustered around the base of *Acacia victoriae* shrubs? Do other ant species show any pattern in nest distribution in relation to the acacia shrubs or the *Iridomyrmex* sp. B nests?

6.2 Methods

6.2.1 Study site

The site for the mapping of ant nests was situated on the Pantapinna track 500 m from the junction with Wirrealpa Rd near Oraparinna in the Flinders Ranges National Park (31° 20.00′ S, 138° 47.95′ E). The area supported ephemeral herbland dominated by the introduced annual *Carrichtera annua* (Wards weed), with a sparse overstorey of generally large *A. victoriae* shrubs and small numbers of other shrub species such as *Senna artemoides* and *Eremophila longifolia*. This area probably supported chenopod shrubs originally, but has been reduced to an ephemeral herbland as a result of overgrazing (Symon 1971). The soil type is a poorly structured red-brown calcareous loam (Swaby 1971) and the area receives an erratic annual rainfall of around 300 mm.

6.2.2 Experimental Design

To determine whether *Iridomyrmex* sp. B nests were clustered around the base of acacia shrubs that contained Homoptera, and whether this affected the positioning of nests of other ant species, the density of nests near the base of the shrubs was assessed and compared with areas further away and with sites distant from any acacia shrubs. This study took place between the 19th and 23rd of April 2004, during which time the maximum daily temperature was between 25 and 35°C.

Three *A. victoriae* shrubs containing *Iridomyrmex* sp. B, which were seen tending Homoptera, were selected (Acacia A-C). These shrubs were at least 30 m from any other shrubs to minimise the chance of foraging trails being linked to other shrubs. For comparison, three areas at least 30 m from any shrubs were chosen as 'No Acacia' sites, within which a stake was randomly placed to mark the mid point.

Iridomyrmex sp. B workers were tracked from the shrub by following their foraging trails. Nest entrances were marked whenever the ants could be seen moving in and out of the ground. The ants were followed until no more connecting nests were found. They appeared to stop within a maximum of 15 m from a shrub if no other shrubs were nearby so a 15 m radius was used as the study area around all shrubs. Nests of all other ant species within the same area were also mapped. The No Acacia areas were searched in a 15 m radius around the randomly placed stake.

Each area was searched for active ant nests at least twice a day e.g. morning and noon, or noon and afternoon, to record hot weather or cooler weather foragers. Six man-hours were spent searching each site. Nests were marked first and then mapped later after the area had been searched again at two times of the day.

All mapping was done with a measuring tape and compass, taking a distance and a bearing to a fixed point, the centre of the bush for the shrubs (marked by a flag) or a stake in the ground at the centre of the circle for the No Acacia sites. A GPS location of each fixed point was taken. Once mapped, samples of the occupiers of the nests were collected and placed in 70% ethanol for identification back at the laboratory.

To illustrate the variability in foraging patterns of *Iridomyrmex* sp. B, the position of ant nest entrances were also mapped in two areas (Acacia D and E) where *Iridomyrmex* colonies were not confined to a single acacia plant and their foraging trails instead linked a number of shrubs. However, these data were not included in the nest density comparison with the No Acacia sites as the position and number of nests were likely to be influenced by the proximity of neighbouring shrubs.

6.2.3 Analysis

The density of ant nests at 1 m radius intervals was calculated for *Iridomyrmex* sp. B and all other ant species combined. Non-linear regressions were fitted to these data using PRISM Graphpad (Version 3.03). Observational records were also made of the active foraging times of the ants and any foraging items they collected.

6.3 Results

The nest entrances of most ant species in this ephemeral herbland habitat were relatively small and indistinct. However, the nests of the various species differed in their size, shape and whether middens of seeds and other materials were found nearby (Appendix 9). There was a very strong relationship between the density of *Iridomyrmex* sp. B (*rufoniger* group) nests and distance from the base of an acacia shrub, with most nest entrances clustered near the base of the shrubs (Figure 6.1). *Iridomyrmex* sp. B workers were seen to forage up into the shrub and along the ground away from shrubs, with foraging trails radiating out along trails of interconnecting nest entrances.

Nests of ant species other than *Iridomyrmex* sp. B were in much lower numbers overall. The pattern of exponential decrease in nest density with distance from the shrub for other ant species was similar to that for *Iridomyrmex* sp. B, but the variability in nest density was much higher within 5 m of shrubs, partly due to a number of samples in which no other ant species' nests were encountered (Figure 6.2.). In contrast, the density of *Iridomyrmex* sp. B nests and other ant species within areas devoid of shrubs revealed no obvious pattern (Figures 6.3. and 6.4.).

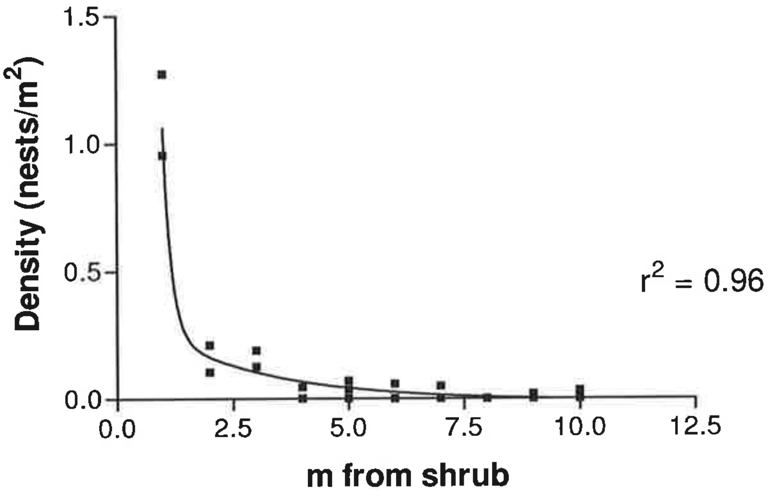


Figure 6.1 Density of *Iridomyrmex* sp. B (*rufoniger* group) nests at distances away from the base of an *A. victoriae* shrub (two phase exponential decay) ($Y=0.4988e^{(-0.4859X)}+8786e^{(-38.14X)}+0.04651$). Mean density of nests in non-shrub areas was 0.017 nests/m^2.

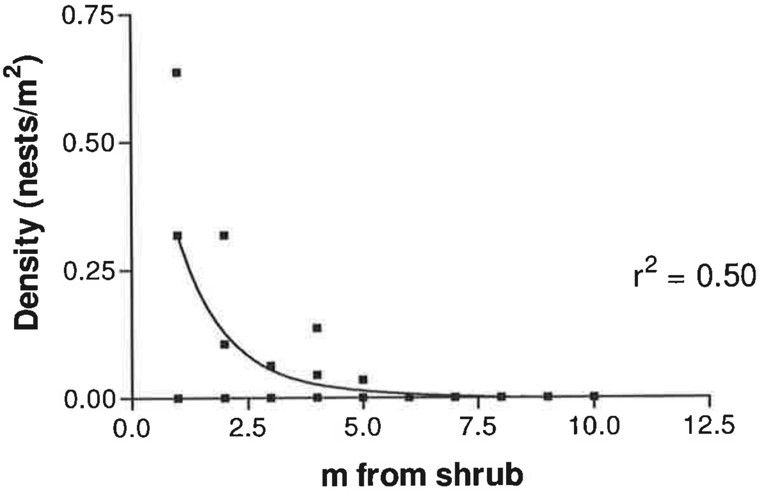


Figure 6.2 Density of other ant nests at distances from the base of acacias (two phase exponential decay) ($Y = 0.05158e^{(-0.2255X)} + 0.7943e^{(-1.019X)} - 0.007761$). Mean density of other ant species nests in non-shrub areas was 0.026 nests/m^2.

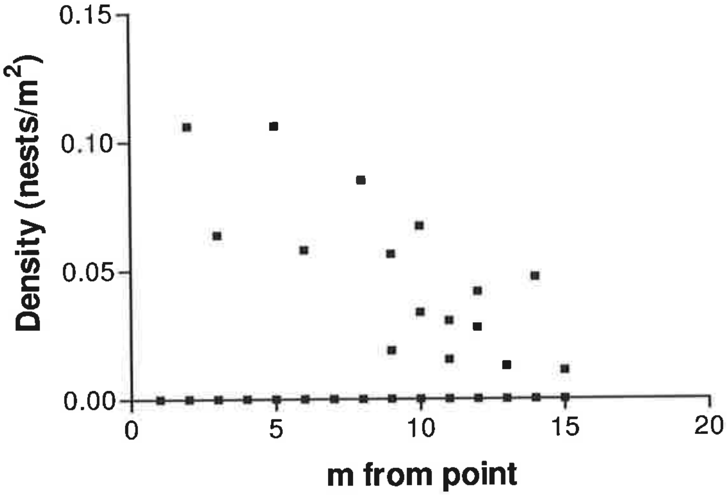


Figure 6.3 Density of *Iridomyrmex* sp. B nests at distances from a fixed random point in No Acacia sites. Mean = 0.017 nests/m^2.

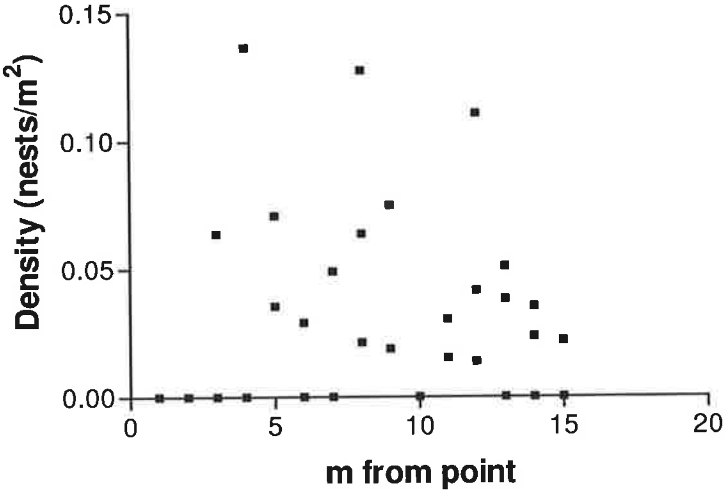


Figure 6.4 Density of other ant nests at distances from a fixed point in No Acacia sites. Mean = 0.026 nests/m^2.

The maximum foraging distance of *Iridomyrmex* sp. B from a shrub varied considerably. Around Acacia C the foraging trails did not extend much further than 5 m from the base of the tree (Figure 6.5c); surrounding Acacia A (Figure 6.5a) and B (Figure 6.5b) they extended to around 15 m, and at Acacia sites D (Figure 6.6a) and E (Figure 6.6b) the colonies spread over a much greater distance and connected to numerous shrubs, not all of which were *A. victoriae*. It was impossible to tell if it was a single colony around each shrub or several.

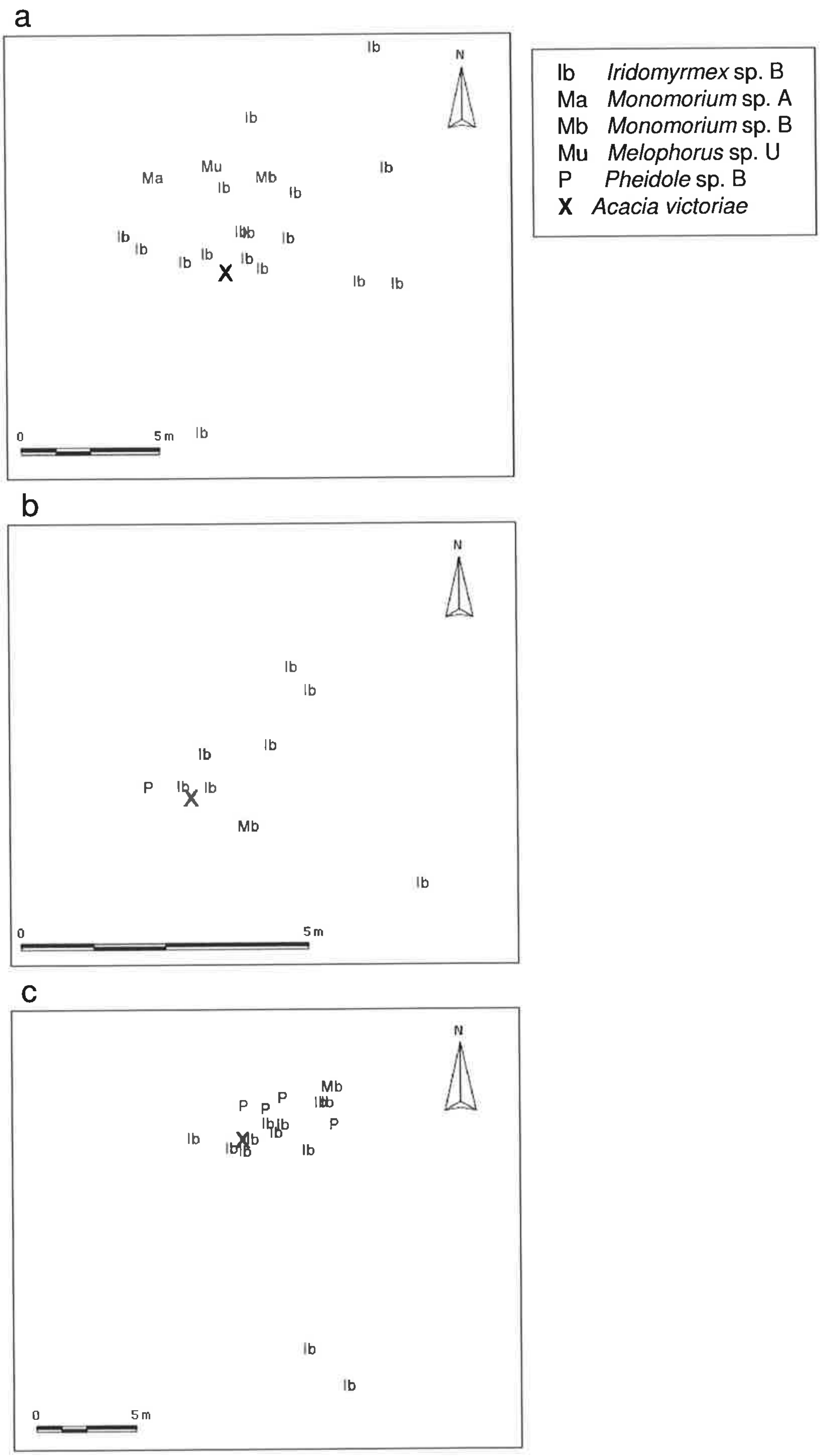


Figure 6.5 Position of all ant species nests within 15 m radius of acacia shrubs a) Acacia shrub A, b) Acacia shrub B and c) Acacia shrub C.

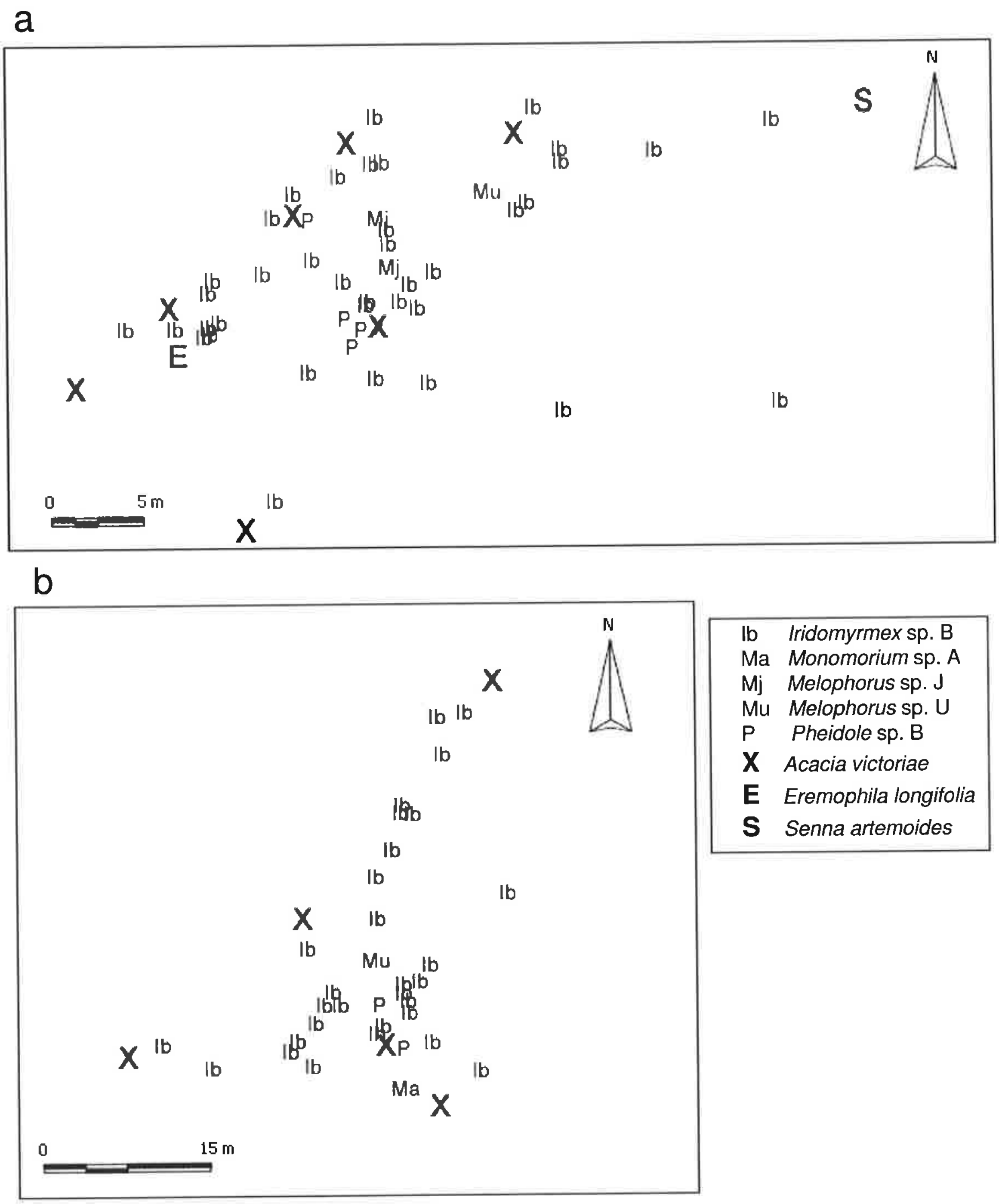


Figure 6.6 Position of *Acacia victoriae, Eremophila longifolia* and *Senna artemoides* shrubs and all ant species nests at **a)** Acacia site D and **b)** Acacia site E.

The ant nests at all three No Acacia sites were uniformly spread within the 15 m radius (Figures 6.7 a-c). Both No Acacia A (Figure 6.7a.) and B (Figure 6.7b.) sites had trails of *Iridomyrmex* sp. B foragers and interconnecting nests that appeared to originate at acacias greater than 25 m away. However, No Acacia C (Figure 6.7c) did not contain any *Iridomyrmex* sp. B nests.

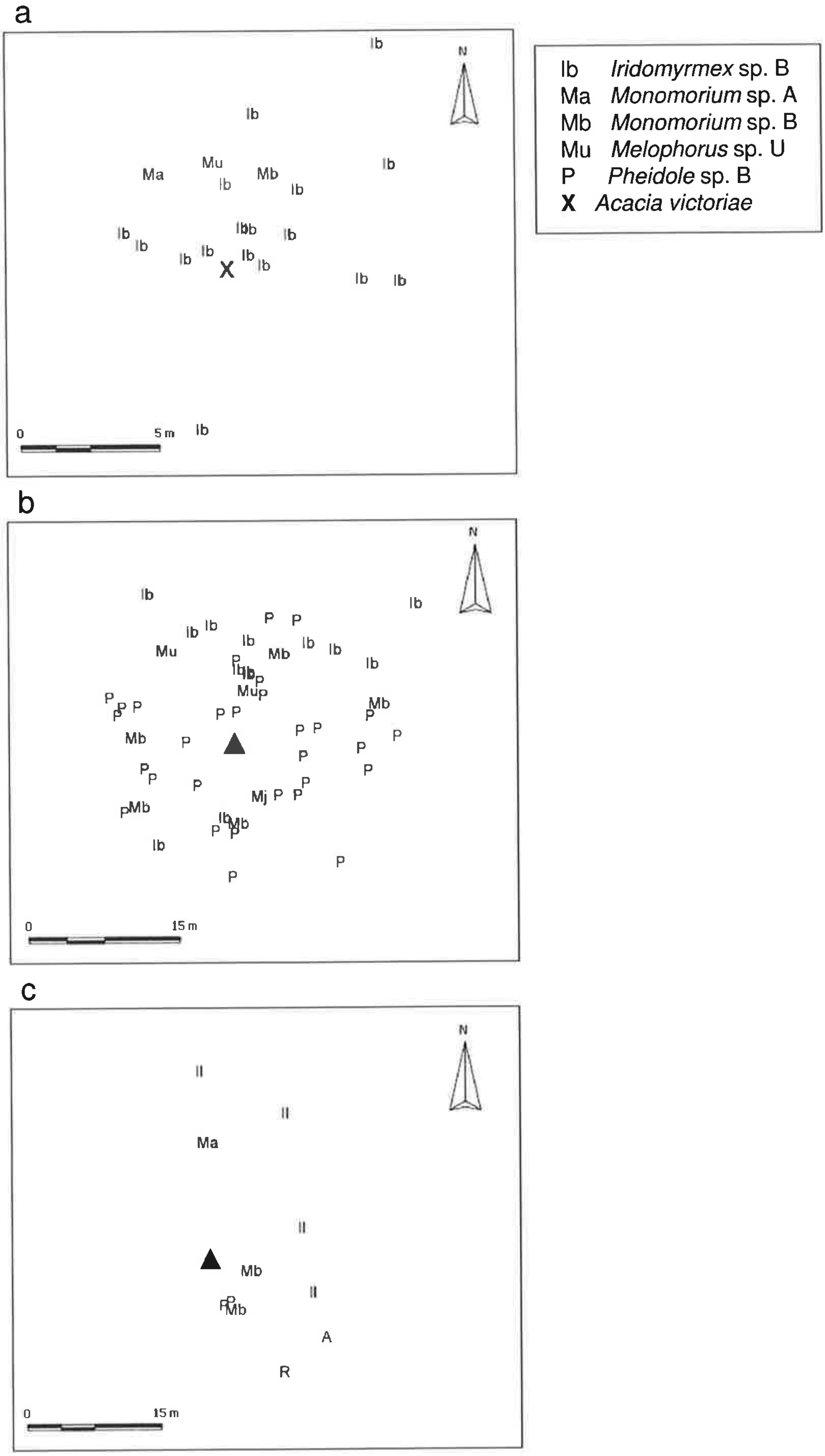


Figure 6.7 Position of all ant species nests within 15 m radius of a fixed point at least 30 m from any *Acacia victoriae* shrubs at **a)** No Acacia site A, **b)** No Acacia site B and **c)** No Acacia site C.

Most *Acacia victoriae* shrubs, and those of two other species, *Senna artemoides* and *Eremophila longifolia*, within this degraded ephemeral herbland site were infested by homopterans and these were frequently tended by ants. Adult and nymph homopterans were found on *A. victoriae* and both appeared to be tended by *Iridomyrmex* sp. B. The most common adult insects were identified as treehoppers belonging to the genus *Sextius* (Membracidae). The species matches the description of *Sextius virescens*, a common species on acacias throughout Australia (Kitching 1974; New 1983; Day 1999). Multiple first instar homopteran nymphs were found in small aggregations encased in loose wax, but could not be assigned to a genus.

At this time of year, *Iridomyrmex* sp. B appeared to do most of its foraging away from the shrubs in the morning and late afternoon when the temperature was cooler. The foraging trails were much more distinct at these times. Little evidence of their trails could be seen in the middle of the day although workers were observed foraging on shrubs at all times of the day (nocturnal foraging was not monitored).

Iridomyrmex sp. B foraging trails were also seen leading from the acacia shrubs and ending at termite nests a couple of metres from the shrubs. *Iridomyrmex* sp. B workers were observed taking termites from these nests during the mornings and returning them to their own nests. The trails to the termite nests ceased in the middle of the day. The collection of termites was especially evident at Acacia site E (Figure 6.6b).

Iridomyrmex lividus, a much larger species, although much less common than *Iridomyrmex* sp. B, was also occasionally seen foraging on *A. victoriae* but was not observed tending Homoptera. Both species were only once seen foraging together on the same shrub, and this was the only other species to be seen on a shrub with *Iridomyrmex* sp. B.

Nests of other ant species were evident around shrubs including two *Monomorium* species (Figures 6.5a-c, and 6.6b), two *Melophorus* sp. (Figure 6.5b, 6.6a and b) and a *Pheidole* species (Figure 6.5a and c, 6.6a and b). These species were not seen foraging on shrubs, but their nests were positioned in relatively close proximity to the *Iridomyrmex* nests. Some temporal partitioning of foraging patterns was observed, with the *Melophorus* species usually the only species seen foraging on the ground in the middle of the day. *Iridomyrmex* sp. B continued to forage on shrubs in the hotter part of the day but foraging trails on the ground were rarely seen at this time. *Pheidole* and *Monomorium* species were only seen foraging in the morning and later in the afternoon.

The numbers of nests of other ant species were much higher in the No Acacia areas (Figures 6.2, 6.4, 6.10-12.) than in the areas around acacia shrubs, and at Site C all nests belonged to species other than *Iridomyrmex* sp. B (Figure 6.12). This was the only site where *I. lividus* and *Rhytidoponera metallica* nests were observed. It is likely that other species forage in these areas but they were not recorded due to their more cryptic nests or behaviour.

6.4 Discussion

The clustering of *Iridomyrmex* sp. B nests around the base of acacia shrubs supporting populations of homopteran insects suggests the importance of honeydew to this small, but behaviourally dominant, species (Cushman and Whitham 1991). It provides further evidence of a relationship between plant and insect carbohydrates and dominant ant colonies (e.g. Davidson 1997; Blüthgen *et al.* 2000; Nash *et al.* 2000) that occurs in a wide range of habitats around the world.

While colonies of *Iridomyrmex* sp. B may be associated with a single acacia shrub, the wide foraging pattern of this species enables colonies to traverse large areas of ground and take advantage of multiple populations of Homoptera on several plants (New 1984). This may allow them to exert their behavioural dominance over a large area. In this environment the numbers of nests of other species were generally low around shrubs but were more numerous at sites away from shrubs, suggesting there may be some level of interspecific competition with, and avoidance of, this dominant *Iridomyrmex* species. This observation parallels evidence from other environments that ants associated with Homoptera tend to be behaviourally dominant species (Room 1971; Samways 1990; Blüthgen *et al.* 2000) and their presence can alter the composition of the surrounding ant community (Blüthgen *et al.* 2000).

One species, *Rhytidoponera metallica,* was found only at the one site without *Iridomyrmex* sp. B. This species is known to be relatively uncompetitive in its interactions with dominant *Iridomyrmex* species (Greenslade 1971) and does not display mass recruitment of workers to available food resources (Griffiths 2005). It is possible that this species avoids nesting near *Iridomyrmex* sp. B colonies to escape this interference competition.

Although not conclusive from this study, the appearance of non-overlapping territories for the two *Iridomyrmex* species may be due to interspecific competition between *Iridomyrmex* sp. B and the larger congeneric species, *Iridomyrmex lividus* or, alternatively, they may have different habitat preferences. The latter species was much less common at the study site, and its nests were not observed near those of *Iridomyrmex* sp. B. Other studies have found strong interspecific competition among *Iridomyrmex* species leading to non-overlapping territories (Greenslade 1976; Fox and Fox 1982; Fox *et al.* 1985; Haering and Fox 1987), and this can also result in a different suite of co-existing ant species within each territory (Greenslade 1976).

A small number of other ant nests were, however, found in the vicinity of acacia shrubs. The higher density of nests of these species and *Iridomyrmex* sp. B may help to explain the high productivity of ants in the Australian arid zone where acacias are common (Andersen 2003); although the exact mechanisms leading to high numbers of other ant species are still unclear. The majority of species that were observed nesting around shrubs were species that would not have to compete directly with *Iridomyrmex* sp. B for food as this species collects liquid carbohydrate or insect protein, and most of the other species found in the area are likely to be seed harvesters (Shattuck 1999; Cooke 2003).

Interference competition from aggressive *Iridomyrmex* towards other species must also be weak enough to allow them to nest and forage in close proximity. A recent experiment found that although *Iridomyrmex* species were able to monopolise baits more often when close to acacia shrubs with populations of Homoptera, *Monomorium* and *Pheidole* species could still access food resources through mass recruitment to baits (Griffiths 2005). For *Monomorium* this access is also possibly enhanced by the use of chemical defences (Griffiths 2005). The positioning of these few nests under shrubs may then be a response to a more shaded and cooler microclimate compared with open areas. *Carrichtera annua* also tends to be larger and produce significant quantities of seed when growing under the shrubs, so access to food resources may also be greater as many of these ant species collect seed (Cooke 2003). *Iridomyrmex* sp. B may also find it more economical to expend energy collecting the honeydew resource than to forcibly prevent other species from establishing nests in the vicinity of the shrubs.

One *Melophorus* species found in the vicinity of shrubs does not appear to be a specialist seed harvester and may have a greater overlap in food resources with *Iridomyrmex* sp. B. However, *Melophorus* are able to avoid competition with the dominant species through their ability to forage for insects in the hottest part of the day (Christian and Morton 1992; Griffiths 2005).

The number of ant species identified in this study is much lower than has been collected in pitfall traps in adjacent areas (Greenslade 1971, see also Chapters 2 and 3). In order to better understand the impact of the availability of liquid carbohydrates and large numbers of dominant *Iridomyrmex* ants on a wider section of the ant community this study would need to be carried out over a wider area, for a longer time and to incorporate nocturnal foragers. The use of pitfall traps as well as nest mapping would also enable the distribution of the more cryptic species to be determined.

Various *Iridomyrmex* species can reach exceedingly high numbers in semi-arid environments but their numerical dominance is not ubiquitous. In comparison with this ant community, other studies conducted within intact semi-arid shrublands have not recorded *Iridomyrmex rufoniger* group species as being an obviously numerically dominant part of the ant community (Dawes-Gromadzki 1999; Read and Andersen 2000; Griffin 2001). This may be related to the presence of acacia or other nectar or honeydew bearing plants. In Western Australia, the numbers of *Iridomyrmex rufoniger* group species were very high in native heath and eucalypt woodland habitats, which are likely to contain plants supplying nectar or honeydew, but they were absent from nearby disturbed farmland (Lobry de Bruyn 1993). Much higher numbers of an *Iridomyrmex rufoniger* species were also collected in an umbrella wattle (*Acacia ligulata*) site in comparison to other nearby arid habitat types (Read 1996). The fact that small *Iridomyrmex rufoniger* group species are in relatively low numbers, if not entirely absent from areas that appear to lack homoptera supporting plants (Dawes-Gromadzki 1999; Read and Andersen 2000; Griffin 2001), suggests that this species may either require some form of liquid carbohydrate to survive, or can only out compete other species where they have access to it.

Anecdotal evidence suggests that acacias and Homoptera infestations on acacias are more common in the degraded ephemeral herbland areas than in nearby intact chenopod shrublands. Homoptera may be more common on acacias in the degraded areas because *A. victoriae* appears to be a 'woody weed' or 'increaser' species. Within remnant shrublands the acacia shrubs are largely confined to drainage lines (Barker 1971), but the degraded herblands contain large numbers of younger, regenerating shrubs. *Sextius* species rapidly colonise young acacias, aggregating on the herbaceous new foliage of young plants (Kitching 1974; New 1984), with ants quickly finding and attending them (New 1983). The herblands also contain many older acacia shrubs that support homopteran populations and these may provide the source of *Sextius* populations for the young shrubs.

Large amounts of carbohydrates are gained by ants from homopteran honeydew but raiding termite nests near acacias would provide *Iridomyrmex* sp. B with the necessary supply of nitrogen for brood production (see review by Hölldobler and Wilson 1990). Ants may also switch from tenders to predators of homopterans if honeydew is of low quality or in high supply and the colony is in need of protein (Cushman 1991). The main life stage of *Sextius virescens* to persist over winter is the eggs (Cookson and New 1980); however, ants may be able to tend other Homoptera species if some remain active during the winter. Ants may also switch to increased collection of protein rich-food such as termites and other insects when homopterans are scarce. They may also collect nectar from extrafloral nectaries or just reduce their foraging efforts in winter with the colder temperatures. A longer-term study over several seasons may be able to ascertain if tending activity by the ants changes with the lifecycle of the homopterans.

In conclusion, sources of liquid carbohydrate from homopteran honeydew appear to be monopolised by a behaviourally dominant ant species in this semi-arid environment, a phenomenon that has been demonstrated in other environments around the world. This association with Homoptera may be responsible for the patchiness of this species. The distribution of this dominant ant also appears to influence the structure of the entire ant community, as nests of some ant species were only found in areas where this dominant species was absent, while others were also in higher densities under acacia shrubs. Together, these results may help to explain the unusually high productivity of ants in the Australian arid zone where acacia shrubs are common.

CHAPTER 7: GENERAL DISCUSSION

This thesis has increased our current understanding of the impact of vegetation structural change resulting from over grazing on arthropod and ant communities. It has therefore contributed to the knowledge of the wider ecological implications of environmental stress in semi-arid systems.

7.1 Congruence of responses across arthropod groups

Many studies have shown relationships between the abundance, diversity or community structure of specific indicator taxa and ecological variables, but their ability to predict changes among other taxa has largely gone untested (Cranston and Trueman 1997). This research has shown that patterns within the ant community associated with habitat type and broad structural differences within habitat types were similarly reflected among the order level epigaeic arthropod community. The species richness of ants across sites was also found to mirror that of the wasp and spider communities. A similar phenomenon of ant species richness correlating positively with the diversity of other arthropod groups has previously been reported (Majer 1983) but this is the first evidence of such a relationship in a semi-arid habitat. These results suggest that ants may be of use as surrogates for the response of other arthropod groups to ecological change which is extremely useful if a group is to be used as an indicator of broader ecological change within an environment (Pearson and Cassola 1992; Andersen 1999). However, these relationships need to be studied in more detail before ants can be confidently used as surrogates for other arthropod groups in semi-arid environments.

7.2 Mechanisms of vegetation impact

Broad scale variation in vegetation communities found within different habitat types in the Flinders Ranges was reflected in differences among the order level arthropod and ant communities. At this scale, ant community structure correlated with a range of environmental variables, including the presence or absence of shrubs, despite such a correlation not being detected in other semi-arid environments (e.g. Whitford *et al.* 1998). Studies of other causes of ecological change within similar environments such as the impacts of mining (Read 1996; Hoffmann *et al.* 2000), fire (Hoffmann 2003) and grazing (Landsberg *et al.* 1999; Hoffmann 2000;

Read and Andersen 2000), or active regeneration of native vegetation during minesite rehabilitation (Andersen 1997a; Majer and Nichols 1998) have found ant communities to be generally unresponsive.

The results of this study suggest that comparing patterns among ant communities can be useful for discerning large-scale ecological differences between sites within these semi-arid habitats. This was found to be the case predominantly at species level but also at functional group level, which is in contrast to the conclusions of Hoffman and Andersen (2003) who found that functional group level responses did not generally reflect habitat differences resulting from disturbance in arid environments.

The differences in arthropod and ant community structure documented here were not correlated with differences in plant species richness at this broad scale, so a range of potentially important abiotic and biotic factors were investigated.

The experimental increase in available structure supplied by plastic plants appeared to elicit little response among the ant community; however, it had a significant influence on the spider community. The increase in structural complexity allowed a diverse range of spiders (from web-builders to ambush predators) to inhabit the ephemeral grassland, with a significant increase in spider abundance, number of families, and species richness. This appears to be a universal response for this group and has been observed in a range of other environments around the world (Hatley and MacMahon 1980; Robinson 1981; Abraham 1983; Greenstone 1984; Rypstra 1986; Gunnarsson 1996; Halaj *et al.* 2000). This experiment reinforces the importance of the abiotic component of structural complexity to this arthropod group.

The strong relationship between spiders and habitat structural complexity suggests that the information this group can supply on the ecological impact of stress and disturbance may be limited, as woody weed shrubs or more desirable shrubs would presumably promote a similar response. However, the importance of biotic resources, such as prey availability, for the long-term maintenance of spider populations that inhabited artificial plants remains to be verified. An extension of the experiment to include independent manipulations of structure and prey would provide information on the relative importance of these two factors for the spider, and perhaps ant, community. It would also be of interest to increase the length of time over which these experiments were conducted to monitor the survival and structure of the communities in the longer term, with and without access to additional prey.

As the structural complexity of the habitat did not appear to be important to the ant community and, on a biogeographic scale, microclimate seems to be the primary abiotic factor influencing ant community composition (Andersen 1995), the importance of shade to the community was investigated. Changes in the foraging activity of a number of ant species were noted after the manipulation of available shade cover within a shrubless habitat using shade cloth tents. An intermediate shade level of around 25%, which is similar to the shade cover found in nearby low bluebush shrubland, corresponded with the highest activity level in these species. The *Melophorus* species may be using the shade as thermal refugia for respite from the heat during intermittent foraging periods in the middle of the day (Christian and Morton 1992), while the other species may be responding to the overall lower temperature from the increased shade that is sufficient to allow them to forage for longer during the day. However, the majority of species within the ant community did not appear to respond during this summer sampling period.

Because a response to the addition of the shade was the exception rather than the rule, in this generally hot and bare environment where access to shade is a limiting resource, it appears that many species within this ant community are not limited by shade, at least during summer. This novel experimental approach has never before been undertaken in semi-arid Australian environments and rarely anywhere in the world. However, this study was limited by its short duration and an extension to incorporate a winter sampling when nocturnal activity is less prevalent, and over a number of years to allow sufficient time for a demographic response, would provide a clearer picture of the importance of this abiotic resource to the rest of the ant community.

One biotic variable that appeared to be closely associated with differences in ant community composition among and within habitats was the availability of homopteran honeydew on *Acacia victoriae* shrubs. The relationship between the patchy distribution of a dominant *Iridomyrmex* species and access to liquid carbohydrates from honeydew was investigated by comparing ant nest densities in areas close to and further away from acacia shrubs. The higher density of nests of *Iridomyrmex* sp. B (*rufoniger* group), in the vicinity of populations of honeydew producing Homoptera indicates that the relationship between dominant ant species and liquid carbohydrates occurs in many different environments around the world (Samways 1990; Blüthgen *et al.* 2000; Nash *et al.* 2000). Variation in the distribution of nests of other ant species in relation to acacia shrubs also suggests a level of interspecific competition with the dominant ant species. Recent work by Griffiths

(2005) has expanded on the results of this study, and found that *Iridomyrmex* sp. B and a larger *Iridomyrmex* species were both more numerous and monopolised more baits when food was placed adjacent to acacias, and this influenced the ability of a range of other ant species within the community to access baits.

The high ant nest density around acacia shrubs provides further evidence for the role of liquid carbohydrates in supporting the highly productive ant colonies of arid Australia (Andersen 2003) and its importance to ant community dynamics generally. The preliminary investigation into this interesting relationship between dominant ants and access to homopteran honeydew provides scope for a wide range of future studies. A survey is also needed to test for correlations between disturbed or over-grazed areas and high numbers of acacia plants with homoptera populations, and high abundances of *Iridomyrmex rufoniger* species, to support the anecdotal evidence gathered here for such a relationship.

7.3 Applications

The differences in order level arthropod and ant community composition among sites with and without shrubs at broad scales, and in relation to various biotic and abiotic habitat variables, suggest that there is a strong relationship between the plant and arthropod communities. Environmental stress-related changes in vegetation structure therefore have broad implications for biodiversity and ecological function. These results, and the fact that arthropods are widespread, abundant and diverse, suggest that changes within arthropod and in particular ant communities can be of use as indicators of the impact of ecological change within semi-arid environments. This information is of interest to land managers as well as ecologists.

While perennial vegetation has been used extensively for land management purposes in these systems (Whitford *et al.* 1998; Landsberg and Crowley 2004), it does not appear to be sufficiently representative of the impact of ecological change on biodiversity more broadly. The inclusion of arthropod groups in monitoring protocols, preferably as part of a suite of biological indicators, would therefore provide more information on the wider impacts of environmental stress and disturbance. This would allow information to be gathered on which components of an ecosystem have improved or become degraded (Whitford *et al.* 1998) and more informed land management decisions to be made.

While monitoring arthropod communities can offer a great deal of ecological information, to be of use to land managers indicator groups must also be practical to use. The similarity in response to broad-scale habitat differences at both ant species and functional group level suggests that identification to species level may not be needed. The suggestion that ant communities may also reflect changes in other arthropod groups also increases their attractiveness as indicators of ecological change as they may be able to act as surrogates for other groups (Pearson and Cassola 1992; Andersen 1999).

Ants and other arthropod groups are increasingly used as indicators of ecological change by land managers (McGeoch 1998; Andersen and Majer 2004). Their usefulness in this regard will only increase as further studies into the impact of ecological change on these groups are undertaken.

Appendix 1: Descriptions of ant functional groups commonly encountered in Australian semi-arid environments based on Andersen (1995).

Functional Group	**Description**
Dominant Dolichoderinae (DD)	Highly abundant, active and aggressive, and able to monopolize resources
Subordinate Camponotinae (Sub-Ord)	Co-occur with Dominant Dolichoderinae to which they are competitively subordinate
Hot Climate Specialists (HCS)	Have behavioural and morphological specializations enabling co-existence with the dominant ants
Cold Climate Specialists (CCS)	Normally restricted to cool and wet regions where Dominant Dolichoderines are absent
Cryptic Species (Crypt)	Forage mostly within soil and litter
Opportunists (Opp)	Have extremely unspecialised behaviour and are poor competitors
Generalized Myrmicines (GM)	Have unspecialised behaviour, but are successful competitors due to rapid recruitment and effective defences
Specialist Predators (SP)	Unlikely to interact with other ants because of their large body size, low population densities and/or specialized diet

Appendix 2: Soil texture (soil type making up the greatest percent in bold), Electrical Conductivity (EC), pH and organic carbon content of top 10 cm soil cores from sites with and without perennial shrubs in the Flinders Ranges.

Site	SHRUB/ HERB	Soil Texture	EC (mS/cm) +/- SE	pH +/- SE	% Organic Carbon (by Walkely and Black titration)
Park 1	SHRUB	clay loam-**silty clay loam**-silty loam	20.85 +/- 4.42	8.23 +/- 0.17	0.334
Park 1	HERB	loam-silty loam	1.37 +/- 0.80	8.56 +/- 0.03	0.430
Park 2	SHRUB	**clay loam**-loam	0.76 +/- 0.07	7.71 +/- 0.12	0.529
Park 2	HERB	clay loam-loam	1.13 +/- 0.07	8.24 +/- 0.10	0.538
Park 3	SHRUB	**clay-loam**-loam	0.99 +/- 0.51	8.62 +/- 0.05	0.449
Park 3	HERB	clay-clay loam-**loam**	1.35 +/- 0.28	8.73 +/- 0.04	0.482
Wirrealpa 1	SHRUB	clay-**clay loam**-loam-sandy loam	0.89 +/- 0.07	8.25 +/- 0.09	0.417
Wirrealpa 2	SHRUB	clay loam-**loam**	1.24 +/- 0.79	8.46 +/- 0.04	0.619
Wirrealpa 3	SHRUB	**clay loam** - loam	1.00 +/- 0.12	8.50 +/- 0.05	0.377
Park	SHRUB		7.53 +/- 2.25	8.19 +/- 0.08	0.437 +/- 0.06
Park	HERB		1.23 +/- 0.1	8.51 +/- 0.05	0.483 +/- 0.03
Wirrealpa	SHRUB		1.04 +/- 0.06	8.40 +/- 0.04	0.471 +/- 0.08

Appendix 3: Species list of ants collected during survey of chenopod shrubland (SHRUB) and ephemeral herbland (HERB) sites in the Flinders Ranges in December 2002.

The functional groups to which the species are assigned are in bold above each list.

Species

Dominant Dolichoderinae

Iridomyrmex agilis
Iridomyrmex ?hartmeyeri
Iridomyrmex lividus
Iridomyrmex ?viridigaster
Iridomyrmex sp. A (*pallidus* group)
Iridomyrmex sp. B (*rufoniger* group)
Iridomyrmex sp. G (*mattiroloi* group)
Iridomyrmex sp. I (*agilis* group)
Iridomyrmex sp. X (*mattiroloi* group)

Sub-Ordinate Camponotini

Camponotus cinereus amperi
Camponotus ephippium
Camponotus loweryi
Camponotus sp. A (*capito* group)
Camponotus sp. F
Camponotus sp. G (*nigroaeneus* group)
Camponotus sp. I (*discors* group)

Cold Climate Specialist

Stigmacros sp. E

Specialist Predators

Cerapachys sp. B (*fervidus* group)
Cerapachys sp. C (*fervidus* group)
Anochetus armstrongi
Bothroponera sp. A (*sublaevis* group)
Pachycondyla lutea

Generalised Myrmicinae

Pheidole sp. B
Pheidole sp. F
Monomorium sp. E (*laeve* group)
Monomorium sp. B (*sordidium* group)

Species

Opportunists

Odontomachus sp. A (*ruficeps* group)
Tapinoma sp. A (*minutum* group)
Ochetellus sp. B
Rhytidoponera ?mayri
Rhytidoponera metallica
Rhytidoponera sp. B (*convexa* group)
Rhytidoponera sp. C (*tyloxys* group)
Tetramorium sp. A (*impressum* group)
Tetramorium sp. C (*impressum* group)
Tetramorium sp. D (*impressum* group)
Tetramorium sp. E
Tetramorium sp. F (*impressum* group)
Tetramorium sp. G (*impressum* group)
Paratrechina sp. A (*obscura* group)

Hot Climate Specialists

Melophorus sp. A (*aeneovirens* group)
Melophorus sp. D (*froggatti* group)
Melophorus sp. L (*pallipes* group)
Melophorus sp. P (*mjobergi* group)
Melophorus sp. U (Group F)
Melophorus sp. V (Group F)
Melophorus sp. W (*wheeleri* group)
Melophorus sp. Y (*fieldi* group)
Melophorus sp. AA (*fieldi* group)
Melophorus sp. AE (*mjobergi* group)
Melophorus sp. AF (*fieldi* group)
Meranoplus sp. H
Meranoplus sp. I (*dimidiatus* group)
Monomorium sp. A (*rothsteini* group)
Monomorium sp. I (*eremophilum* group)

Appendix 4: Spider species collected in pitfall traps and from artificial structures placed in ephemeral herbland in the Flinders Ranges.

ID	Family	Species	Foraging type	Hunting type	Preferred foraging stratum
BK	Araneidae	*Argiope protensa*	Web	Web	Foliage
CM	Araneidae	*Eriophora* sp. A	Web	Web	Foliage
BX	Clubionidae	*Cheiracanthium* sp. A	Hunter	Active	Foliage/Ground
CG	Clubionidae	*Cheiracanthium* sp. B	Hunter	Active	Foliage/Ground
CL	Clubionidae	*Cheiracanthium* sp. C	Hunter	Active	Foliage/Ground
BV	Corinnidae	*Supunna picta*	Hunter	Ambush	Ground
BL	Corinnidae	Juvenile	Hunter	Ambush	Ground
BM	Corinnidae	sp. A	Hunter	Ambush	Ground
CD	Corinnidae	Juvenile	Hunter	Ambush	Ground
CN	Deinopidae	*Deinopis* sp. A	Web	Web	Foliage
BT	Dictynidae	*Callevophthalmus* sp. A	Web	Web	Ground
CI	Dictynidae	*Callevophthalmus* sp. B	Web	Web	Ground
BY	Gnaphosidae	*Eilica* sp. A	Hunter	Ambush	Ground
Q	Gnaphosidae	*Eilica* sp. B	Hunter	Ambush	Ground
AF	Gnaphosidae	sp. A	Hunter	Ambush	Ground

Appendix 4: cont.

ID	Family	Species	Foraging type	Hunting type	Preferred foraging stratum
BP	Gnaphosidae	Junevile	Hunter	Ambush	Ground
CO	Gnaphosidae	Junevile	Hunter	Ambush	Ground
M	Gnaphosidae	Junevile	Hunter	Ambush	Ground
B	Lamponidae	*Lampona ampeinna*	Hunter	Ambush	Ground
CP	Linyphiidae	*?Australolinyphia* sp. A	Web	Web	Foliage
BJ	Lycosidae	*Pardosa serrata*	Hunter	Ambush	Ground
K	Lycosidae	Junevile	Hunter	Ambush	Ground
L	Lycosidae	Junevile	Hunter	Ambush	Ground
AL	Oonopidae	*Grymeus robertsi*	Hunter	Ambush	Ground
BW	Oonopidae	sp. A	Hunter	Ambush	Ground
BD	Oxyopidae	*Oxyopes* sp. A	Hunter	Ambush/active	Foliage
BE	Oxyopidae	*Oxyopes* sp. B	Hunter	Ambush/active	Foliage
BF	Oxyopidae	*Oxyopes* sp. C	Hunter	Ambush/active	Foliage
BG	Oxyopidae	*Oxyopes* sp. D	Hunter	Ambush/active	Foliage
BH	Oxyopidae	*Oxyopes* sp. E	Hunter	Ambush/active	Foliage

Appendix 4: cont.

ID	Family	Species	Foraging type	Hunting type	Preferred foraging stratum
BI	Oxyopidae	*Oxyopes* sp. F	Hunter	Ambush/active	Foliage
CF	Oxyopidae	*Oxyopes* sp. G	Hunter	Ambush/active	Foliage
D	Oxyopidae	sp. A	Hunter	Ambush/active	Foliage
O	Oxyopidae	sp. B	Hunter	Ambush/active	Foliage
BU	Prodidomidae	sp. A	Hunter	Ambush	Ground
BC	Salticidae	*Grayenulla wishartorum*	Hunter	Active	Foliage/Ground
AK	Salticidae	*Lycidas chrysomelas*	Hunter	Active	Foliage/Ground
BA	Salticidae	*Lycidas* sp. A	Hunter	Active	Foliage/Ground
AH	Salticidae	sp. A	Hunter	Active	Foliage/Ground
CH	Salticidae	sp. B	Hunter	Active	Foliage/Ground
N	Salticidae	sp. C	Hunter	Active	Foliage/Ground
P	Salticidae	sp. D	Hunter	Active	Foliage/Ground
Y	Salticidae	sp. E	Hunter	Active	Foliage/Ground
CJ	Theridiidae	*Achaearanea* sp. A	Web	Web	Foliage
BS	Theridiidae	*Euryopis* sp. A	Web	Web	Foliage

Appendix 4: cont.

ID	Family	Species	Foraging type	Hunting type	Preferred foraging stratum
CK	Theridiidae	*Latrodectus hasselti*	Web	Web	Foliage
AB	Theridiidae	*Steatoda* sp. A	Web	Web	Foliage
V	Zodariidae	*Habronestes* sp. A	Hunter	Active	Ground
BR	Zoridae	Junevile	Hunter	Active	Ground
CA	Zoridae	Junevile	Hunter	Active	Ground
CB	Zoridae	Junevile	Hunter	Active	Ground

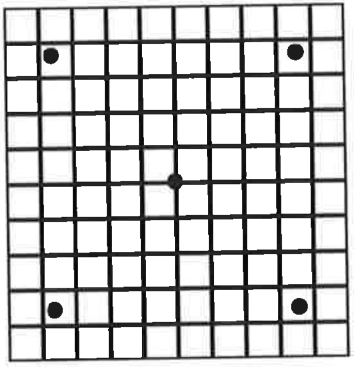
Appendix 5: Percent shade cover (number of shade tents) assigned to each plot during experimental addition of shade to ephemeral herbland.

BLOCK 1		BLOCK 2		BLOCK 3	
Plot	% Cover	Plot	% Cover	Plot	% Cover
1	0	1	10	1	20
2	25	2	15	3	30
5	45	5	20	4	25
6	5	6	25	6	35
9	35	7	0	8	10
11	40	9	35	9	15
12	10	0	30	10	45
13	20	12	30	11	5
14	30	13	40	14	40
16	20	15	50	16	50

Appendix 6: Arrangement of shade tents for each shade cover level added in experimental plots in ephemeral herbland.

Grey shaded squares indicate the position of shade tents. Black circles indicate approximate position of pitfall traps.

0 %



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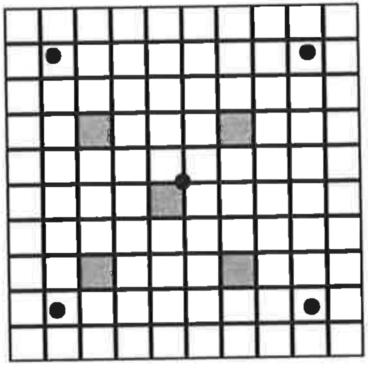

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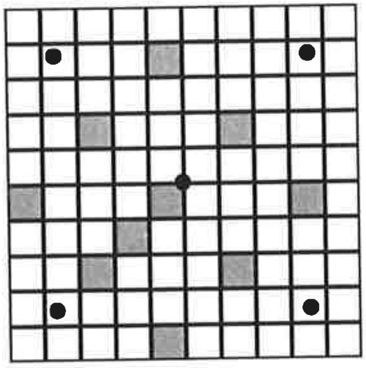

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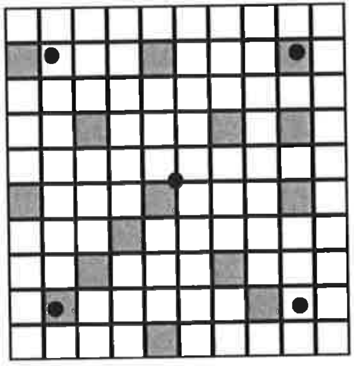

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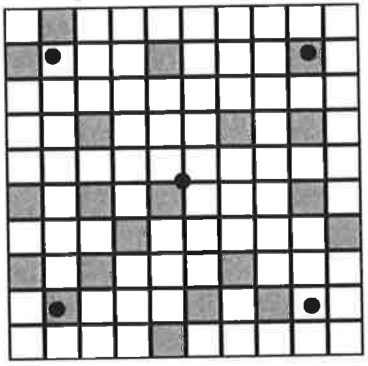

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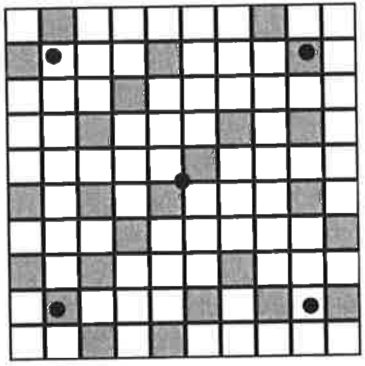

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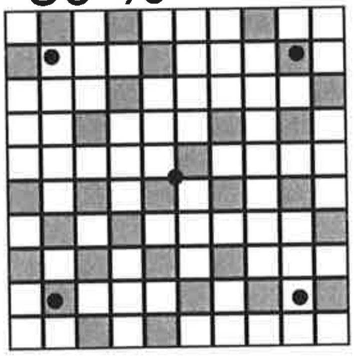

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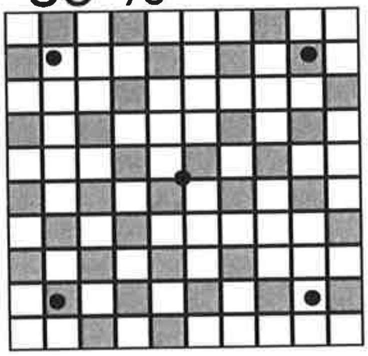

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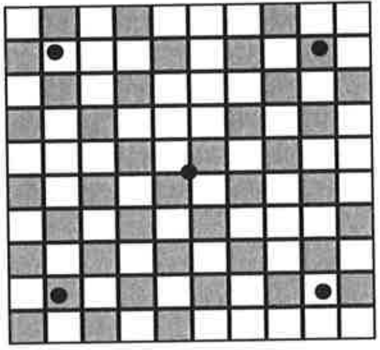

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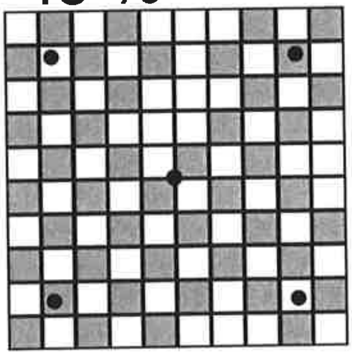

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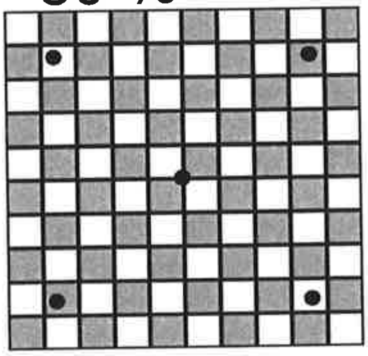

Appendix 7: Summary of ant community data collected from all plots combined in summer 2002 prior to manipulation of shade cover in ephemeral herbland.

Maximum number of individuals collected in a single plot, minimum collected and 75th quartile.

Taxa	Maximum	Minimum	75th quartile
Functional Groups			
Dominant Dolichoderinae	6418	3	189.8
Generalised Myrmicinae	440	2	67.5
Opportunists	13	0	4
Hot Climate Specialists	442	10	106.8
Specialist Predators	5	0	1
Genera			
Iridomyrmex	6418	3	189
Melophorus	194	10	94.3
Pheidole	283	2	42
Rhytidoponera	11	0	3
Tetramorium	4	0	1
Monomorium	410	0	20.5
Species			
Iridomyrmex sp. B	6402	3	145.3
Pheidole sp. B	194	0	12
Pheidole sp. H	238	0	25.8
Melophorus sp. U	168	4	85.5
Melophorus sp. J	40	0	9.8
Melophorus sp. D	19	0	0

Appendix 7: cont.

Taxa	Max	Min	75th quartile
Species			
Anochetus armstrongi	5	0	0
Rhytidoponera metallica	8	0	0.8
Monomorium sp. L	410	0	5
Tetramorium sp. J	4	0	1

Appendix 8: Regression coefficients (r^2) for all non-linear regressions of abundances of ant species, genera and functional groups in pitfall traps in response to increased shade levels in 2003.

None of the linear regression results were significant ($p<0.05$). All data n = 30, Maximum data n = 11, 75th Quartile n = 5. Those in bold have relatively high r^2 values for both maximum and 75th Quartile.

Taxa	Linear (all data)	Gaus-sian (all data)	Linear (max only)	Gaus-sian (max only)	Linear (75th Quartile)	Gaus-sian (75th Quartile)
Functional Groups						
Dominant Dolichoderinae	<0.001	0.003	0.002	0.024	0.104	0.105
Generalised Mymicinae	0.055	0.057	0.074	0.17	0.503	0.600
Opportunists	<0.001	<0.001	0.036	0.082	0.024	0.181
Hot Climate Specialists	0.028	0.069	0.065	**0.32**	0.376	**0.889**
Specialist Predators	0.039	0.25	0.096	**0.61**	0.645	**0.911**
Genera						
Iridomyrmex	<0.001	0.003	0.002	0.024	0.104	0.105
Melophorus	0.054	0.085	0.13	**0.41**	0.355	**0.933**
Pheidole	0.033	0.057	0.56	**0.35**	0.202	**0.283**
Rhytidoponera	<0.001	0.004	0.058	0.098	0.043	0.129
Tetramorium	0.020	0.40	0.006	**0.51**	0.003	**0.743**
Monomorium	0.056	No fit	0.085	0.10	0.620	0.864
Species						
Iridomyrmex sp. B	<0.001	0.002	0.002	0.023	0.104	0.105
Pheidole sp. B	0.004	0.004	0.004	0.076	0.072	No fit
Pheidole sp. H	0.045	0.29	0.058	**0.70**	0.104	**0.946**

Appendix 8: cont.

Taxa	Linear (all data)	Gaussian (all data)	Linear (max only)	Gaussian (max only)	Linear (75^{th} Quartile)	Gaussian (75^{th} Quartile)
Species						
Melophorus sp. U	0.050	0.084	0.13	**0.45**	0.369	**0.920**
Melophorus sp. J	0.045	0.068	0.13	0.19	0.321	0.643
Melophorus sp. D	<0.001	0.057	0.003	0.30	No fit	No fit
Anochetus armstrongi	0.046	No fit	0.10	**0.63**	0.690	**0.940**
Rhytidoponera metallica	0.002	No fit	0.014	No fit	0.085	No fit
Monomorium sp. L	0.061	No fit	0.081	0.082	0.495	0.996
Tetramorium sp. J	0.017	0.40	0.041	**0.89**	0.133	**1.00**

Appendix 9: Description of ant nests observed within semi-arid ephemeral herbland with scattered *Acacia victoriae* shrubs.

Species	**Description of nest**
Iridomyrmex sp. B (*rufoniger* group)	Small circular holes (1-2 mm diameter) in the ground into which workers enter and emerge. Workers moved between many nest entrances interconnected by foraging trails spanning 10's of metres.
Iridomyrmex lividus	Small turrets of soil approximately 4 cm high with interconnecting nests covering 10's of metres allowing them to forage over large areas.
Monomorium sp. A (*rothsteini* group) and sp. B (*sordidium* group)	Tiny circular holes (approx. 0.5 mm diameter) in the ground, sometimes with a pile of *Carrichtera annua* seeds nearby.
Pheidole sp. B	Holes in the ground a bit larger than those of the *Monomorium* spp. (1-2 mm diameter). No middens of seeds present nearby.
Melophorus spp. J (*wheeleri* group) and U (*fieldi* group)	A hole in the ground (approx. 2 mm diameter) with a piles of debris (seed husks etc.) in a crescent-shape situated a few centimetres from the nest entrance
R. metallica	Slit shaped nest entrance on top of a slight mound approximately 1 cm high.

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