

Synergistic impact of invasive alien plants and the  
alien Argentine ant on local ant assemblages in the  
Western Cape

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Thesis presented in partial fulfilment of the  
Requirements for the degree of Master of Science (Entomology)  
at the  
University of Stellenbosch

Stellenbosch  
January 2008

## DECLARATION

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

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## ABSTRACT

Alien trees, *Pinus* spp. and *Eucalyptus* spp., affect ants negatively in the Cape Floristic Region (CFR), a global biodiversity hotspot in South Africa. They reduce ant abundance and species richness, thus also changing ant assemblage structure. This is alarming, because almost 1300 species of plant species in the CFR are dispersed by certain indigenous ants, and thus there is concern for an indirect effect on indigenous plant assemblages. One of the most impacting ant species on seed dispersal is the invasive Argentine ant (*Linepithema humile* (Mayr)), which discards seeds outside its nest, where they do not germinate. Ten sites, on Vergelegen Wine Estate, were selected to explore these effects of alien plants. These varied from invaded to non-invaded sites. Each site consisted of six sampling points, which in turn consisted of four pitfall traps left out for seven days, during December 2005, February 2006, May 2006 and September 2006. Forty species of ant were sampled, and various analyses used to illustrate the comparative effects of plant invasion. All analytical methods showed that invasive alien plants had a significant impact on the abundance and richness of the ant species assemblage, by creating a dense canopy cover that changed the abiotic environment of the epigaeic ants' habitat. Furthermore, increased alien tree invasion correlated significantly with Argentine ant abundances. The Argentine ant displaced *Pheidole capensis* and *Camponotus* spp., while it decreased the abundances of commonly-occurring indigenous ants, such as *Lepisiota capensis* and *Plagiolepis* spp. Displacement by the Argentine ant may be a result of indirect competition for food resources. The effects of invasive aliens are synergistic in that there is a cascade effects from initial plant invasions to subsequent animal invasion.

## OPSOMMING

Indringer bome, *Pinus* en *Eucalyptus*, affekteer miere op negatiewe wyse in die Kaap Florsitiese Streek (KFR), 'n area in Suid Afrika van belang t.o.v. globale biodiversiteit. Hierdie uitheemse indringer bome verminder hulle hoeveelheid en spesies rykheid. Die bogenoemde is kommerwekkend omdat meer as 1300 plant spesies in the KFR versprei word deur miere. Die verandering in hoeveelheid en versameling van inheemse miere kan dus ernstige implikasies hê op die saad verspreiding van inheemse plant spesies. Een van die mees verwoestende effekte op saad verspreiding is veroorsaak deur die indringer Argentynse mier (*Linepithema humile* (Mayr)), wat sade neer werp buite hulle neste, waar hulle nie suksesvol kan ontkiem nie. Tien monsterings-tereine was geselekteer om die bogenoemde effekte te ondersoek op Vergelegen Landgoed. Hierdie het afgewissel van indringer tot skoon tereine. Elke terrein is op ses versamelings-plekke gemonster, met vier pitvalle, wat oopgelê het vir sewe dae gedurende Desember 2005, Februarie 2006, Mei 2006 en September 2006. 40 spesies van miere was gemonster. Indringer plante het 'n betekenisvolle impak gehad het op die hoeveelheid en rykheid van die mier gemeenskappe, deur die skepping van 'n dig baldakyn wat die abiotiese omgewing van die miere se habitat verander het. Die vermeerdering van indringer plante veroorsaak die vermeerdering van Argentynse miere. Kanonieke Mede-Respons Analise illustreer dat die Argentynse mier *Pheidole capensis* en *Camponotus* spp. verplaas het, terwyl dit ander inheemse mier getalle verminder het, soos *Lepisiota capensis* en *Plagiolepis* spp. Die verplasing deur die Argentynse mier mag die resultaat wees van indirekte wedywering vir hulpbronne. Die effekte van indringer species is dus sinergisties deur dat 'n kaskade effek ontstaan vanaf plant tot dier indringer spesies.

## ACKNOWLEDGEMENTS

Firstly, I wish to thank my supervisor, Michael Samways for inspiring me to do this project in the first place and for always setting time aside to help me. Even when he was extremely busy, he never refused a question and was always patient and ready with advice. I wish to thank Gerald Wright and Vergelegen Wine Estate for granting me access to their entire farm, and also for their help and assistance in gathering information. Brigitte Braschler, Carmen Boonzaaier, Emile Bredenhand helped me with identification. Pia Addison trusted me with the Department's ant collection which was of great help for the final identification.

I would like to thank CIB for their financial support, and for providing the opportunity to present my work at their research meetings, and for some good parties.

René Gaigher, John Simaika, and Emily Arlette Apinda-Legnuou: how can I thank you enough for all the advice, encouragement and all the good times in the Merlot Lab? Sven Bourquin helped me with statistics. Melodie McGeoch, Pat Reavell, Colleen Louw and Henk Geertsema were always ready to listen to a story or two – at some stages of this study on a daily basis!

My “moedertjie” (Mia Schoeman), “pappie” (Jan Schoeman) and my “sissie” (Juanie Schoeman) are my best friends. I want to thank the rest of my family. One cannot ask for better. My other family, the Norbertines in Kommetjie and the Carmelite Sisters in Retreat have supported me through their encouragement and prayers.

Together with that great company in Heaven, they have been my strength and stay.

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CHAPTER ONE  
INTRODUCTION

## 1.1 GENERAL THREATS POSED BY INVASIVE ALIEN PLANTS

Aliens are a major threat to biodiversity (Wilcove *et al.*, 1998) and a major cause of extinctions globally (Clavero & Garcia-Bertha, 2005). About 700 000 ha of US wildlife habitat are being invaded every year, with species having adverse effects on biodiversity (van Wilgen *et al.*, 1996). They also pose enormous costs to agriculture, forestry and fisheries (Wittenberg *et al.*, 2001).

However, evidence supporting a general and primary role for invasive aliens in extinctions remains limited (Gurevitch & Padilla, 2004). With climate change predicted to play such a prominent role in the future (Botes *et al.*, 2006), it would be safe to say that the increase of invasive alien plants in the landscape would have a synergistic role in changing ecosystems. This could ultimately lead to species extinctions.

The effects of aliens are varied and complex and affect native species and their interactions in different ways (Samways, 2005). Nevertheless, aliens can transform native ecosystems by using excessive amounts of resources (water and oxygen), by adding resources (nitrogen), by suppressing fire and accumulating leaf litter, as well as changing hydrology (Le Maitre *et al.*, 1996; Gorgens & Van Wilgen, 2004). Ecosystems are especially affected by alien tree species used in commercial forestry and agroforestry, because of the widespread planting of a small number of species in different parts of the world (Richardson, 1998), and their subsequent spread into native habitats without human aid.

### 1.1.1 Alien trees in riparian habitats

Alien trees are a key impact on dragonfly assemblages (Samways & Taylor, 2004) with assemblages being able to recover when these aliens are removed (Samways *et al.*, 2005) as habitat quality is returned. Specialist species are especially affected. In highly degraded environments, the number of dragonfly species decrease, with the disappearance of sensitive specialists, while generalist species often remain (Samways, 2006).

### 1.1.2 Alien invasive plants in fynbos

South Africa is a country with major alien plant problems (Richardson & van Wilgen, 2004). Of the eight terrestrial biomes in South Africa, the fynbos is the best studied and most invaded. There are dense invasions in the mountains and lowlands and along all major river systems. Three genera of trees and shrubs pose a major threat: *Acacia* spp., *Pinus* spp. and *Hakea* spp. (Richardson & van Wilgen, 2004). A study by Higgins *et al.* (1999) indicated that invasive aliens have a far greater potential distribution range than is currently realized. Parts of the Cape Peninsula have an 89 % cover of invasive alien plants. The species richness of an area and that area's potential to be invaded are positively correlated (Higgins *et al.*, 1999).

*Pinus pinaster* Aiton alone threatens hundreds of endemic species (Higgins *et al.*, 1999). At least three other species of *Pinus*, with self-perpetuating invasive populations over large areas of the Cape Floristic Region (CFR) are *P. patula* Masters, *P. halepensis* Miller, and *P. radiata* Don. Richardson and Higgins (1998) further point out that the extent of the problem will increase over the next few decades if left unchecked.

Alien trees can affect local arthropod assemblages (Samways *et al.*, 1996) by changing aspects of the faunal community and can influence hilltopping behaviour (Lawrence & Samways, 2002). Donnelly & Giliomee (1985) and Manders (1989) found that the abundance and species richness of ants was lower in pine plantations than in native fynbos habitats. Other research has shown that dense stands of alien trees and shrubs in fynbos can rapidly reduce abundance and diversity of native plants (Richardson *et al.*, 1989; Holmes *et al.*, 2000), which affects the native arthropod fauna. Yet, little is still known about how alien trees affect insects and other arthropod assemblages in the CFR, especially in view of it being a global biodiversity hotspot (Myers *et al.*, 2000).

There is a growing body of evidence suggesting that alien tree plantations support much lower biodiversity than indigenous areas. Samways *et al.* (1996) found that species richness of invertebrates in pine and eucalyptus plantations was lower than that of indigenous forests but not significantly so. Ratsirarsan *et al.* (2002) found that ant species richness was marginally higher in pine plantations than in indigenous forests of the Cape peninsula. This may be attributed to the fact that the indigenous forests in the area have

higher chances of local ant species extinctions because of the small patch size and isolation of the indigenous forests. This finding is important, because focus is increasingly being drawn to areas that have remnant habitat patches for conservation (Boonzaaier *et al.*, 2006). Many remnant patches of fynbos are only surviving as discreet patches between vineyards, or as remnants along dirt road verges. Arguable, the best-preserved and most extensive fynbos patches survive on the highest elevations of mountainous areas and their slopes, where agricultural impact is still minimal.

Giliomee (2003) suggested that the CFR is low in insect species richness relative to its plant diversity. However, this may be an illusion as so many taxa have been inadequately sampled in the region. Indeed, the CFR has many endemics that are uniquely adapted to survive the harsh conditions of the CFR including the natural patch dynamics of fynbos. Many insects in fynbos are adapted to small and extremely localized areas (*Colophon* beetles and many lyceanid butterflies). Many of these butterfly species have specialized mutualistic relationships (Botha & Botha, 2006).

Insects adapted to certain conditions and microhabitats generally cannot adapt to environments much different from the habitats in which they evolved. A slight change in temperature, in wind speed, in shading or leaf litter, could have an effect on stenotypic species in particular.

Invasive alien species facilitate some of these changes in the following ways:

1. Invasive alien plants change the inherent vegetation type of the landscape (Samways, 2005).
2. Invasive alien plants can outcompete other plants utilized by local insects (Samways, 2005).
3. Invasive aliens in the CFR are predominantly large woody trees, a plant form or architecture not normally associated with Fynbos except in ravines. *Pinus*, *Eucalyptus* and others, throw shade over a wide area by forming a dense canopy cover and decreasing temperatures, and a change in leaf litter, type, depth and quality. Soil moisture and structure also change (MacDonald *et al.*, 1985).

4. Invasive alien plants create conditions unsuitable for specialist herbivorous insects, on which specialist predators in turn depend (French & Major, 2001).

5. Invasive alien plants facilitate other invasions by animals, such as by the Argentine ant (*Linepithema humile*), an important invasive species (Boonzaaier, 2006; Luruli, 2007).

## 1.2 ECOLOGICAL IMPORTANCE OF ANTS IN THE CFR

Ants (Formicidae) were used for this study because they are abundant, diverse and functionally important, and ant assemblages are sensitive to disturbance (Anderson *et al.* 2002). Ants can be sampled and studied reliably, because ants have restricted foraging ranges and perennial nests (Agosti *et al.*, 2000). They have also been used to assess invertebrate assemblage responses to alien plants (Donnelly & Giliomee, 1985), and as bio-indicators of habitat fragmentation, especially in the species rich rainforest ecosystems of South-east Asia (Brühl *et al.*, 2003).

Ants are also important ecologically because 1300 species of plants within the CFR are dispersed by ants (Bond & Slingby, 1983). Indigenous ants fulfil other important ecological functions, such as pollination, nutrient recycling, soil and soil layer improvement and predation of insect pests (Addison, 2004). Within natural undisturbed areas, there is a clumping of ant nests, clustered near predictable sources of abundant seeds supporting many native ant species (Dean, 2006). The altered abundance and composition of native ant communities due to invasive plants can have implications for the seed dispersal functions of native plants (French & Major, 2001).

Many plant species in the CFR have seeds with elaiosomes that chemically mimic animal tissue (Handel & Beattie, 1990) and are attached externally to seeds of these plant species and promote dispersal of the seeds by ants (Witt & Gilliomee, 2004). These myrmecochorous seeds are located by ants and transported to their nests, where the elaiosomes are eaten and the undamaged seeds are discarded either within the nest or on the soil surface (Horvitz, 1981). The dispersal of seeds, decreased pressure from competition, protection from fire and avoidance of seed predators are the advantages that

increase the germination rates of myrmecochorous plants in ant nests (Witt & Giliomee, 2004). Both *Anoplolepis* and *Pheidole* build subterranean nests with galleries and channels well suited to seed storage, away from fire and predators, and in which seeds germinate and seedlings become established (Bond & Slingsby, 1984).

One of the emerging themes in recent years has been the effect that Argentine ant (*Linepithema humile*) plays in the ecology of fynbos (Witt *et al.*, 2004; Witt & Giliomee, 2004; Luruli, 2007). This ant is considered one of the world's most destructive invasive species, and has spread throughout Mediterranean-type environments across the world (Holway *et al.*, 2002; Lach, 2007; Luruli, 2007) and is associated with the displacement of important native myrmecochorous ant species, even in pristine fynbos habitats (Witt *et al.*, 2004), through direct and indirect competition for food resources. They also affect entire habitats, by disrupting seedling recruitment of myrmecochorous plants (Bond & Slingsby, 1984). The disruption of an ant fauna can have profound effects on the density, dispersion and reproduction of endemic plants (Pudlo *et al.*, 1980). Native ants transport seeds to their nests before feeding on elaiosomes. In contrast, *L. humile* moves seeds for very short distances and does not take them into nests. The seeds remain vulnerable after dispersal (Bond & Slingsby, 1984).

### 1.3 AIMS OF THIS STUDY

The main objectives of this study are as follows:

- to assess and document the environmental attributes of Vergelegen, a site in the Western Cape with a wide variety of natural patches and disturbance regimes all in close proximity;
- to assess levels of impact of invasive alien trees relative to land use and study the effects these may have on the local ant fauna; and in particular to explore the changes in insect assemblages impacted by invasive alien plants, especially *Pine* and *Eucalyptus*, and by the invasive Argentine ant (*Linepithema humile*);

- to highlight the importance of remnant fynbos patches for the conservation of ants and other insects.

This study should provide the Vergelegen Wine Estate and the surrounding farms with a decision support system. This will contribute to environmental management strategy on other wine farms in the area.

CHAPTER 2  
SITES AND METHODS

## 2.1 BACKGROUND

### 2.1.1 Historical and Social

Vergelegen (S 34.05482, EO 18.92911) (Dutch for ‘situated far away’) is a farm 3000 hectares in size, with a history of human presence stretching back to 1685 when the Governor of the Dutch East India Company instructed Commander William Adriaan van der Stel to relocate the company’s outpost to the Hottentots Holland Mountains. Van der Stel initiated the intensive agricultural activities on the farm, including vine and fruit cultivation, as well as introducing sheep and cattle. After six years, the farm boasted a half a million vine stocks. In 1706, the directors of the Dutch East India Company dismissed him and ordered him to return to the Netherlands. Thereafter, Vergelegen passed through a succession of owners until 1798, when the Theunissen family took ownership of it for over a century. The estate was purchased by the PUNCHI Barlows in 1941. The estate remained in the family’s possession until purchased by Anglo American Farms Ltd in 1987 (Vergelegen Wine Estate, 2007).

Vergelen has experienced a wide variety of farming activities over the past 40 years. However, some of the higher elevation areas have not been actively farmed for the last 15 years. Owing to the effects of wind distribution of seeds, combined with the impacts of wild fires, which increases the spread of alien plants, the fynbos habitat has been invaded by alien woody plants over the last few years (AmFarms, 1988).

### 2.1.2 Climate

Vergelegen is situated in the Helderberg Kom, which has a Mediterranean Climate with hot dry summers (December to February) and rain during autumn and winter (March to August) (AmFarms, 1988). Average rainfall is 600 mm per year, most of which falls during winter, and average temperatures during harvest season is 27 °C (Rouseau, 2007).

### 2.1.3 Soil

The estate has 20 different soil types, of which the main topsoil horizon is Orthic A horizon, darkened by organic matter. Orthic or ‘normal’ soils occur over virtually the full range of soil farming conditions encountered in South Africa. Canals have been built to

drain the large amount of surface runoff water, which otherwise would cause major soil erosion problems (AmFarms, 1988).

#### 2.1.4 Livestock

The keeping of is livestock was seen as a viable economic activity. However, Vergelegen has intensive pastures with grass, with these grasses starting to become invasive in adjoining natural areas (AmFarms, 1988).

#### 2.1 5 Timber and windbreaks

In 1988, before extensive land clearing was undertaken, approximately 500 ha of mountain area in Vergelegen abutting the Hottentots Holland Nature Reserve were planted with timber. Of the total production, only 35 ha of timber were deemed reasonable at the time (AmFarms, 1988). Vergelegen has a history of wind-related damage. Because wind is considered to have a negative impact on the growth, production and quality of deciduous and citrus fruit, windbreaks were planted (AmFarms, 1988). The plantation and windbreaks of pine and bluegum have become invasive, with trees spreading up the slopes of the Hottentots Holland Mountains, contributing significantly to the spread of invasive aliens on the Estate.

#### 2.1.6 Fire management and the clearing of invasive alien plants

Vergelegen has taken specific measures to control wild fires on the estate, which includes the clearing of alien plants and integrating it with fire management and protection. Vergelegen implemented their management plan during the time that this study was undertaken. In recognition of their work in invasive alien plant removal, the Estate has been awarded the “First Champion of the Wine and Biodiversity Initiative.” The alien invasive removal programme on Vergelegen Estate is not the only one of its kind. The Working for Water programme was started in 1995 to conduct and coordinate alien plant management throughout South Africa and leads the way in alien plant management in natural and semi natural areas (Richardson & van Wilgen, 2004; DWAF, 2007).

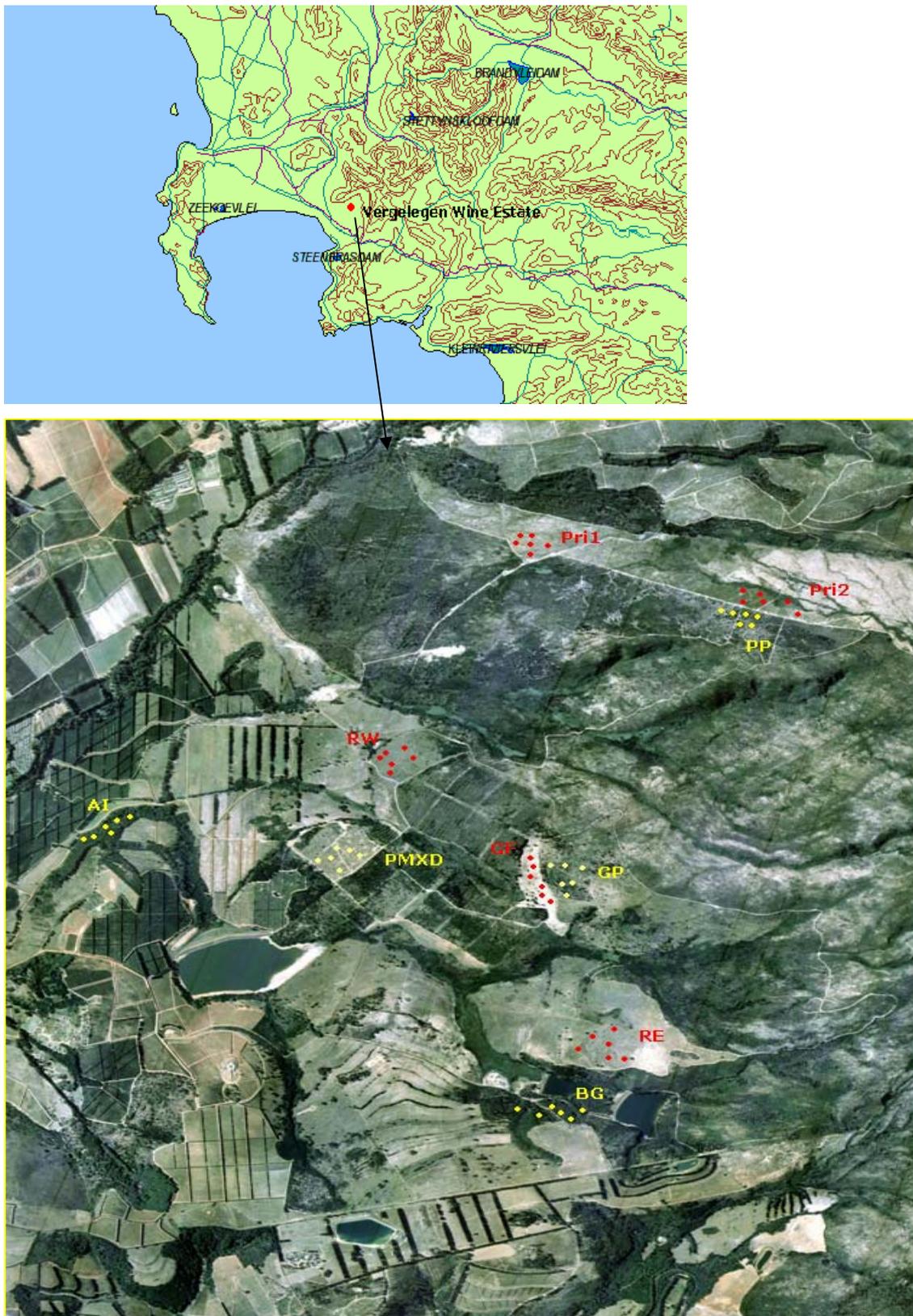


Fig. 1. Site map of Vergelegen Wine estate situated in the heart of the Cape Winelands showing positions of sites and individual sampling points per site. The red squares indicate those sampling points at sites invaded by alien trees, while the yellow squares indicate the positions of sampling points in uninvaded sites.

## 2.2 SITE SELECTION

In selecting the sites for this study, the management units as set out in the farm's management plan were kept in mind, and those sites where invasive alien clearances were not to take place between November 2005 and December 2006 were specially selected as ideal for this study.

Ten sites were selected to represent various gradations of invasiveness, from natural habitats (N –sites) to completely invaded habitats (CI –sites). The sites were selected in terms of common plant architecture, history and relative position to other areas which differed in plant composition. These sites were divided into four groups, based on the dominant plant type: completely natural uninvaded fynbos (N), renosterveld (R), fynbos sites invaded or planted with pine tree (PN), and sites that were completely invaded by *Eucalyptus* (CI).

Each of these sites is now discussed in more detail.

### 2.2.1 Habitat Type: Pine and persisting fynbos (PN)

#### 2.2.1.1 Site 1: Upper Pine Site

This area was situated between the open fynbos area (undisturbed fynbos sites 6 and 7, section 2.2.3.1) and the dense pine plantations along the Hottentots Holland Mountains. This area was densely infested with alien plants, with very few indigenous plants growing beneath the pine trees (fig. 2). The most common invasive alien plants that occurred in the sampled area were *Pinus pinaster* Aiton, *P. radiata* Don, *Acacia longifolia* Willd. and *Hakea* spp.



Fig. 2. Habitat densely invaded by pine trees, with persistence of low growing, indigenous Asteraceae.

#### 2.2.1.2 Site 2: Pine mixed with fynbos (GP)

This site was situated along the dirt road across the whole southern slope of the ridge ascending Langkloofberg (fig. 3). This management unit was heavily infested. Some remnant fynbos plants however, remained. The pine trees at this site were relatively dense and tall. The invasive aliens at the site were *Acacia saligna* Wendl., *P. radiata*, *P. pinaster* and *Hakea spp.*, with the pine trees however the most dominant of the alien assemblage.



Fig. 3. Fynbos area planted with pine trees for timber along the upper slopes of Langkloofberg.

#### 2.2.1.3 Site 3: Pine mixed with Fynbos 2 (PMXD)

Situated atop the hill in Rooiland Dam, this was an area dense with invasive alien plants, mainly pine trees (*P. pinaster* and *P. radiata*) (fig. 4). Other invasive plants included *A. longifolia*, *A. mearnsii* De Wild. and *Eucalyptus* spp. The site selected is completely

surrounded by a firebreak, and in those areas of the site where the pines (the trees were approximately 10 years of age at the time of the study), did not occur in such dense stands, which allowed some indigenous vegetation to grow.



Fig. 4. Old fynbos habitat planted with pine trees, for timber production.

#### 2.2.2 Habitat Type: bluegum trees (*Eucalyptus* spp.) sites (CI)

##### 2.2.2.1 Site 4: Lower invasive site (AI)

An area close to the managed section of the farm was also selected for sampling. The dense forest of alien trees along the furrow leading to the Estate's main road was selected (fig. 5). The most common invasive aliens were *Eucalyptus cladocalyx* Muell., *Populus canescens* Aiton, *Solanum mauritianum* Scopoli and *Acacia saligna* .



Fig. 5. Old bluegum site situated close to fruit tree orchards.

##### 2.2.2.2 Site 5: Bluegum site (BG)

The bluegum forest on the slopes of the lower narrower dam on the estate was selected, which as a site was completely covered in bluegum trees (fig. 6). There was no

undergrowth, as it had been cleared previously. The leaf litter covered the ground completely. The site selected for sampling consisted entirely of large and mature *Eucalyptus cladocalyx*.



Fig. 6. Bluegum site; the ground layer has a thick leaf litter layer.

### 2.2.3 Vegetation Type: Natural uninvaded Fynbos (N)

#### 2.2.3.1 Sites 6 and 7: Undisturbed fynbos (Pri1 and Pri2)

This area was along the Lourensford Estate boundary, and a road divided the upper and lower areas. The area had not been cultivated. The fynbos was low to medium height (0.2-0.5 m). Vegetation densities vary from sparse (Pri1) (fig. 7) to older and denser (Pri2) (fig. 8). The area was vulnerable to *Acacia* spp., pine and hakea invasion.



Fig.7. Undisturbed fynbos site 1 was at an elevation of  $\pm 193$  m.a.s.l.



Fig. 8. Undisturbed fynbos site 2 was at an elevation of  $\pm 237$  m.a.s.l.

#### 2.2.3 2 Site 8: Relic Fynbos site (GZ)

This site was in the same management area as the above site, and was separated by the pine plantation along the upper slopes of the mountain (fig. 9). It runs for approximately 200 m along the road running past a pine plantation (GP) and was 20-50 m wide before being hedged in by close-growing stands of pine trees. The soil surface was arid and bare. The fynbos varied from low growing plants ( $\pm 0.2$  m), to high dense stands of *Protea* spp. and *Leucadendron* spp.



Fig. 9. A relict area of fynbos on the upper slopes of Langkloof berg. Pine plantations surrounded the entire site. The plants are very old ( $\pm 12$  years), as the site has not been burned in recent years.

#### 2.2.4 Vegetation Type: Renosterveld (R)

##### 2.2.4.1 Site 9: *Renosterveld site 1 (RW)*

This was a recovered area of fynbos. The fynbos consisted mostly of Asteraceae, growing 0.3 – 0.5 m and quite dense (fig. 10). There was no infestation of woody plants.



Fig. 10. Renosterveld site 1, situated close to pine plantations on Hottentots Holland Mountains.

##### 2.2.4.2 Site 10: *Renosterveld site 2 (RE)*

This was the open field above the vlei land area, surrounded by dense infestations of alien trees. This area was used for livestock grazing (prior to 1995), but fynbos plants, especially Asteraceae have recovered considerably.



Fig. 11. Renosterveld site 2, situated close to vineyards on the Estate.

## 2.3 FIELD TECHNIQUES

### 2.3.1 Sampling techniques

The epigaeic ant fauna was sampled using pitfall traps. The problems of pitfall trapping include the disturbance of soil in the sampling points, which may chase certain species away. This disturbance effect was countered by leaving the traps for a week after being dug before sampling was commenced. Overall, this is an effective technique for sampling epigaeic ant assemblages (Read and Anderson, 2000; Agosti *et al.*, 2000), and is considered a reliable approach for comparative sampling (Boonzaaier *et al.*, 2007). Six sampling points were selected within each of the ten sites. The sampling points were spaced between 30 – 50 meters apart from each other depending on the size of the habitat patch selected as a site.

Each sampling point consisted of four pitfall traps spaced 1 m from each other, forming a square. The pitfall traps used were plastic containers 12 cm deep with a lip diameter of 9 cm. Plastic cups with lips that could fit around the circumference of the containers were used for easy placement and removal (Fig. 12).

Ethandiol was used as the liquid preservative in each trap. Ethandiol has various advantages above other liquids used for such studies; it is relatively safe, it does not attract or repel ants because of its lack of odour, and it helps to preserve the insects' sampled (Agosti *et al.*, 2000).

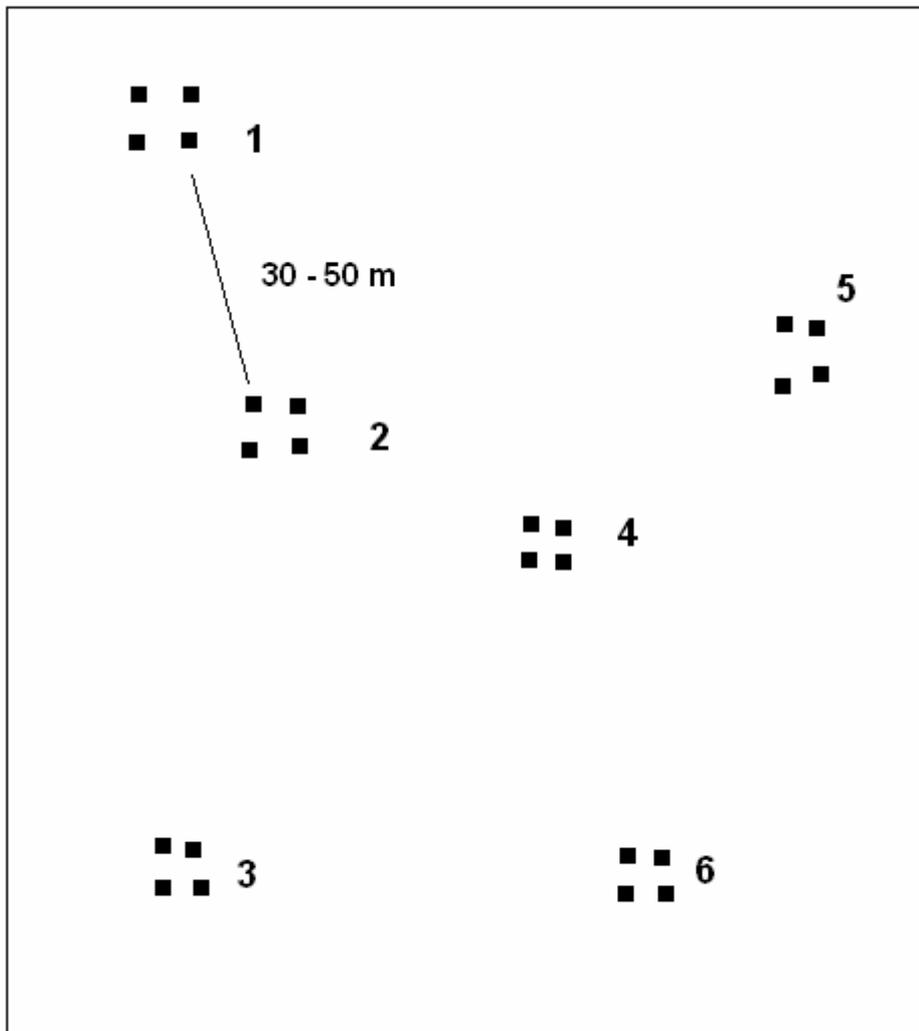


Fig. 12. General position of sampling points per site, and representing one habitat type, and showing distance between the sampling points. Each square represents one pitfall.

Each trap was left out for seven days per sampling season; i.e.: sampling point BG1 (the first trap sampled in the bluegum site), was sampled for exactly the same amount of time during December 2005, February 2006, May 2006 and September 2006 (in other words, all sites would be sampled once with pitfalls left out for seven days in December 2005, and once again for 7 days in February etc.). This ensured that a larger sample size was collected, larger than could be obtained using hand sampling. Hand sampling was done initially, but yielded a far too low abundance of ants for the purposes of this study. The same sampling method was used throughout the all sampling points, of which there were, in total, 240 pitfall traps spaced across Vergelegen Estate. Each set of pitfall traps or sampling point throughout the study were sampled in exactly the same way during the sampling times chosen to represent the seasonal effects of the passing year.

### 2.3.2 Specimen processing

As the specimens in the traps were mixed with soil and plant debris, it was important to separate out the specimens from this material as soon as possible to avoid deterioration. Each jar was labelled carefully with its field number, and the excess ethanidiol was poured off. The samples were then washed with water, then 70 % alcohol. These were then stored in jars with 70 % alcohol, making them ready for sorting.

Manual sorting was done with the aid of a stereomicroscope and forceps. The contents of the jar were poured into Petri dishes. The specimens were manually picked out with forceps, and in the case of very small and delicate ants, with a fine paintbrush. The bulk of the specimens were either ants or spiders. As this study was only on ants, the bycatch of spiders and other invertebrates was stored for possible future use.

The specimens were then recognized to morphospecies, where the individuals were grouped according to distinctive morphological characteristics.

Identification was done in one continual session, using a voucher collection stored in vials and mounted on a card on which the field number, date, sampling season, species code, identifying features was written and a simple illustration of some of these features was drawn. Different specimens from successive samples that were the same morphospecies were placed on one card, in order to see whether each morphospecies was one or possibly more actual taxonomic species. In those cases where one morphospecies yielded more than one taxonomic species, I went back and redid the samples where these lumped morphospecies occurred and split them then according to their actual taxonomic species.

### 2.3.3 Data processing

A species-by-sample data matrix was constructed from the above. The cells in the matrix contain abundance data, of a particular ant species (row) at a given sampling point (column).

From the data matrix, singletons and doubletons, as well as uniques (species known from only one sample) and duplicates (species known from more than one sample) were identified.

### 2.3.4 Environmental variables

The following environmental variables were measured:

1. Upper canopy shading, measured in percentage shading on the ground;
2. Leaf and organic matter depth, measured in centimetres;
3. Leaf and organic matter cover measured in percentage area of pitfall quadrant;
4. Elevation, taken from the Geographic Positioning System (GPS) and measured in meters;
5. Degree of naturalness (Table 1. ;)
6. Vegetation type (Kent and Coker, 1992) (Table 1. ;)
7. *Linepithema humile* was also included as an environmental variable, as it was found in preliminary sampling to have a major influence on the whole ant assemblage.

Table 1. Degree of naturalness and vegetation type (observed environmental variables).

DEGREE OF NATURALNESS				
1. Completely covered with invasive alien plants, with no indigenous fynbos plants left.	2. Major disturbance of invasive alien woody plants, with fynbos persisting at much reduced densities.	3. With some disturbance of invasive alien plants, but remaining fynbos at low densities.	4. Relatively natural fynbos, with alien species present, but at very low density Recovered fynbos of pasture land left fallow.	5. Completely natural, with the fynbos without any invasive plants in vicinity. With no history of disturbance
VEGETATION TYPE				
1. Woodland, or plantations, including trees over 5 m tall. Predominantly pine and bluegum.	2. Scrub type (1.0 – 5.0 m), includes scrub, shrubs and saplings.	3. Field layer type (0.2 – 1.0 m), includes tall grasses, herbs and some low fynbos plants.	4. Open ground type (less than 0.2 m) includes bare ground.	5. Edge, dirt road verges.

## 2.4 DATA ANALYSIS

### 2.4.1 Species accumulation curves and estimated species richness

Species accumulation curves were undertaken using estimateS (Colwell, 2005). Mean abundance and species richness was calculated for uninvaded fynbos (N), renosterveld (R), fynbos planted with pine trees (PN) and bluegum (CI).

Estimates of local species richness using non-parametric techniques based on the distribution of individuals among species were done (Colwell & Coddington, 1994). This estimate is a measure of the sampling sufficiency for the habitat type using the selected sampling technique.

Colwell & Coddington's (1994) *Chao1* estimator was used to calculate estimated ant species richness for each season.

$$S_{chao1} = S_{obs} + F_1^2/2F_2$$

Where  $S_{obs}$  = species observed;  $F_1$  = number of observed species represented by a single individual, and  $F_2$  = number of observed species represented by more than one individual.

#### 2.4.2 Assemblage similarity and dissimilarity

The sampling units were defined *a priori* (beforehand based on field observations) as uninvaded fynbos (N), renosterveld (R), fynbos planted or invaded by pine trees (PN) and habitats taken over by bluegum trees (CI). These groupings were later confirmed by an Analysis of Similarity (ANOSIM) test using PRIMER 05©. ANOSIM is a nonparametric permutation procedure that operates on a similarity (Bray-Curtis similarity) worksheet. It allows a statistical test of the null hypothesis that there are no differences between groups of samples (Clarke & Gorley, 2001).

Pairwise comparisons were made between the above-named four groups (N, R, PN and CI). The pairwise R-values give an absolute measure of how separate the groups are.

The results for the ANOSIM was then compared to CLUSTER dendrograms, which attempt to identify and group similar species assemblage patterns in habitat clusters during different seasons. This was achieved with the CLUSTER function in PRIMER 05©, using summed fourth-root transformed data.

Clustering was performed on Bray-Curtis similarity matrices, using group average linkage, to produce dendrograms. The data were square-root transformed to remove heterogeneity of variance. This was done in an attempt to see whether Formicidae assemblages respond to broad changes in the dominant vegetation assemblage, and whether the results found for the ANOSIM analysis would correspond roughly to the results for the CLUSTER analysis.

An important practical requirement of the above analysis was to identify which species primarily account for the observed assemblage differences (Clarke & Gorley, 2001).

The species assemblages chosen *a priori* were then identified with SIMPER analysis. This method examines the percentage contribution each species makes to the average dissimilarity between the samples that are similar in plant vegetative regime, and by doing so, can identify species or assemblages of species that typify a group. The data were not standardized, and was fourth-root transformed, showing species that contributed overall to 90 % of the sampled abundance.

Average abundance for ant species illustrated the structure of ant assemblages per field type during the sampling seasons in tabular form.

#### 2.4.3 Canonical Correspondence Analysis (CCA)

Multivariate analysis of ant abundance data was done, and ordination diagrams with the environmental variables were undertaken, using the CANOCO© software program.

CCA is a direct gradient analysis technique that uses multiple regressions to select linear combinations of environmental variables that account for most of the variation in the species scores on each axis. Therefore the diagram relates visually the pattern of variation between species, environmental variable and in sampled areas or sampling points (Sharratt, 2005; Lepš & Šmilauer, 2003).

Detrended Correspondence Analysis (DCA) was done initially containing only species data in order to see which analysis would be used. Thus, linear and unimodal models can be used, depending on the results for the gradient analysis. It was difficult to decide *a priori* about which family of ordination methods to use, so it was recommended that the heterogeneity of the species data be determined, using the lengths of the community composition gradients in species turnover units, as calculated by DCA (Lepš & Šmilauer, 2003).

It is important to note that rare species were not downscaled, and the data were transformed by correcting them to logarithmic values. A Monte-Carlo permutation test was also conducted to explain variation and show the significance of the environmental variables, and the significance of the 1<sup>st</sup> and both axis together in explaining the variation found in the ordination diagram (Lepš & Šmilauer, 2003). Scaling was selected for

between species distances, as these ordination diagrams illustrated the separation of species very well, as explained by some of the measured environmental variables.

CCA ordination diagrams were used to display the distribution patterns underlying species and field type as explained by the environmental variables (Sharratt, 2005). Spearman's rank order correlation (STATISTICA© software program) was used to explore the impacts of the environmental variables on separate species per season (Grant & Samways, 2007).

The analysis that followed from this was with Argentine ant (*Linepithema humile*) abundance was included as an environmental variable. This was done to see whether there is a positive or negative relationship between Argentine ant and the selected environmental variables, as Argentine ant, in being influenced by abiotic variables, may in turn act as a biotic variable that impact on local indigenous ant assemblages. This could illustrate a cascade effects from plant to invertebrate invasion potential.

## CHAPTER 3

### RESULTS

### 3.1 OVERALL SPECIES RICHNESS AND ABUNDANCE

In total, 40 species and 11 994 individuals were sampled. Species accumulation curves show that for all seasons combined (Fig. 13.), and for separate sampling seasons (Figs 14, 15, 16 & 17), the plot has reached a near asymptote. The sampling was therefore largely representative of each sampling season, as well as for all sampling seasons together. Observed species richness for all samples using Colwell and Codington's (1994) species estimator approached 99 % of the estimated species richness.

Five subfamilies were sampled: Cerapachinae, Dolichodorinae, Dorylinae, Formicinae and Myrmicinae. Dolichodorinae had only two, but abundant species (2877 individuals), while the Cerapachinae (two species, two individuals) and Dorylinae (one species, three individuals) were rare. Myrmicinae (20 species, 8078 individuals) and Formicinae (15 species, 1065 individuals) were the most species rich and overall most abundant subfamilies sampled. The most species rich genus was *Camponotus* (11 species, 307 individuals), and the most abundant genus was *Tetramorium* (eight species, 1885 individuals).

The averages of ant species diversity per habitat type over the sampling period show that there were differences in species richness per habitat type. The number of species found per season reflected the assumed trends: the natural fynbos sites yielding a higher richness than the pine and bluegum sites (Fig. 18). All habitat types, with the exception of the bluegum (CI) sites, showed a slight drop in species richness from February 2006 to May 2006. Richness increased between May 2006 and September 2006. The most species rich time of year was during the summer (February 2006 sampling time). There was, however, considerable standard deviation in richness (Table 2) especially for natural fynbos (N) samples, where the species richness obtained was extremely variable, with some of the fynbos samples yielding very high ant richness, and other samples yielding a lower richness.

The average ant abundances per season per sampling period showed that the natural fynbos sampling points yielded higher abundances of ants throughout the year, especially during May 2006 (Fig. 19). Standard deviations again are large for natural sites (N and R) and sites invaded by bluegum sites (CI) (Table 3).

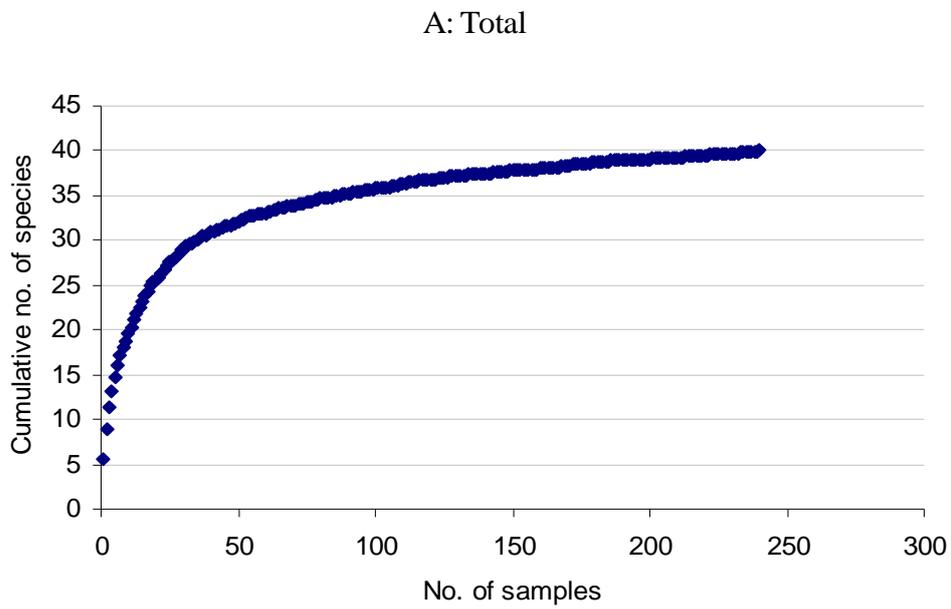


Fig. 13. Species accumulation curve for all Formicidae, sampled over the whole sampling period. A total of 240 samples, yielding 11 994 specimens were sorted into 40 species.

B: December 2005

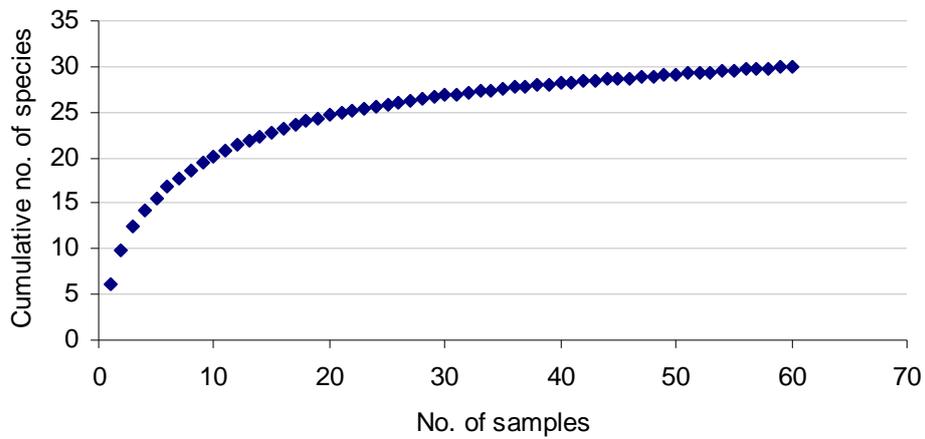


Fig. 14. Species accumulation curve for Formicidae, sampled during December 2005.

C: January 2006

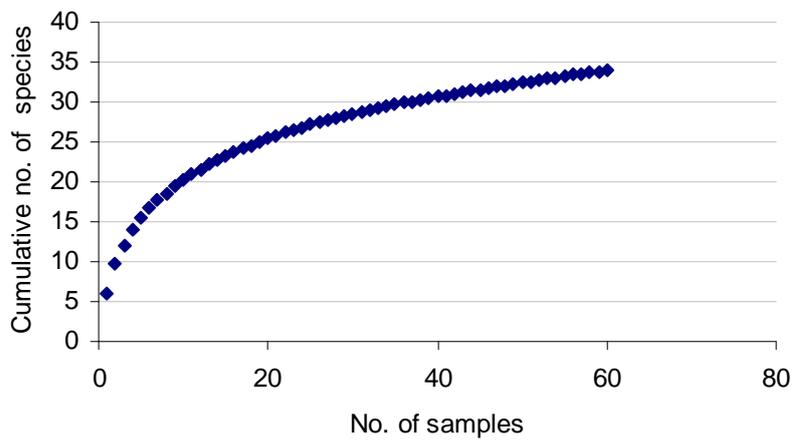


Fig. 15. Species accumulation curve for Formicidae, sampled during February 2006.

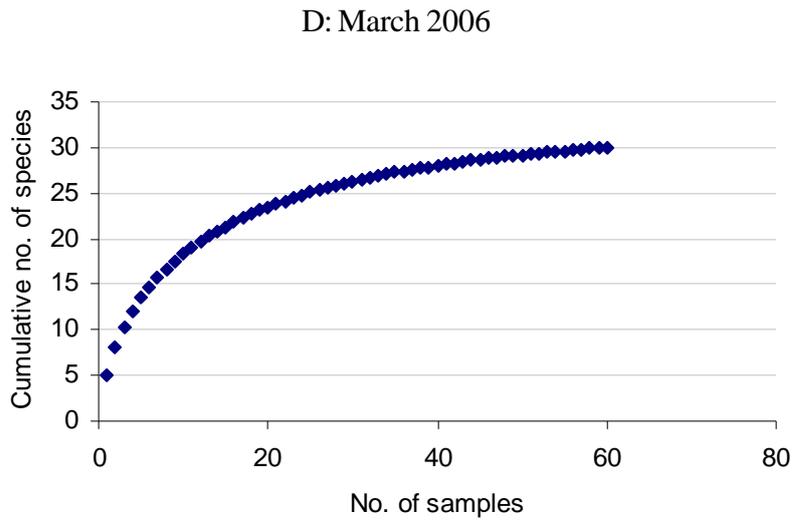


Fig. 16. Species accumulation curve for Formicidae, sampled during March 2006.

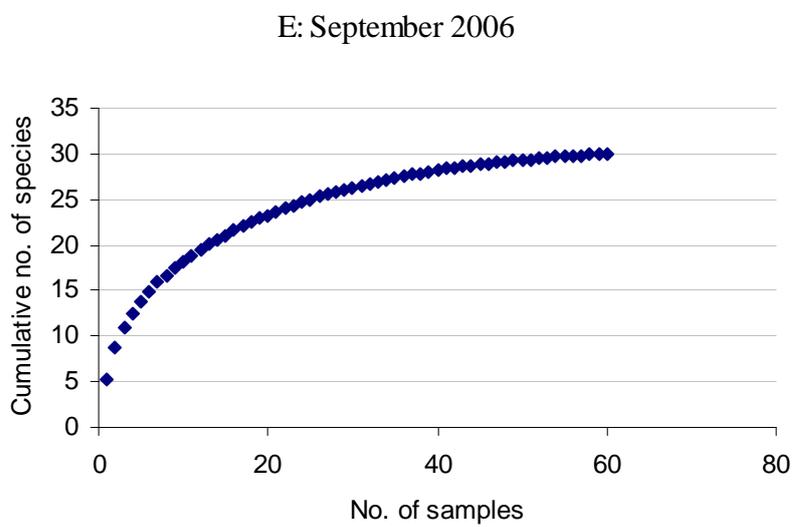


Fig. 17. Species accumulation curve for Formicidae, sampled during September 2006.

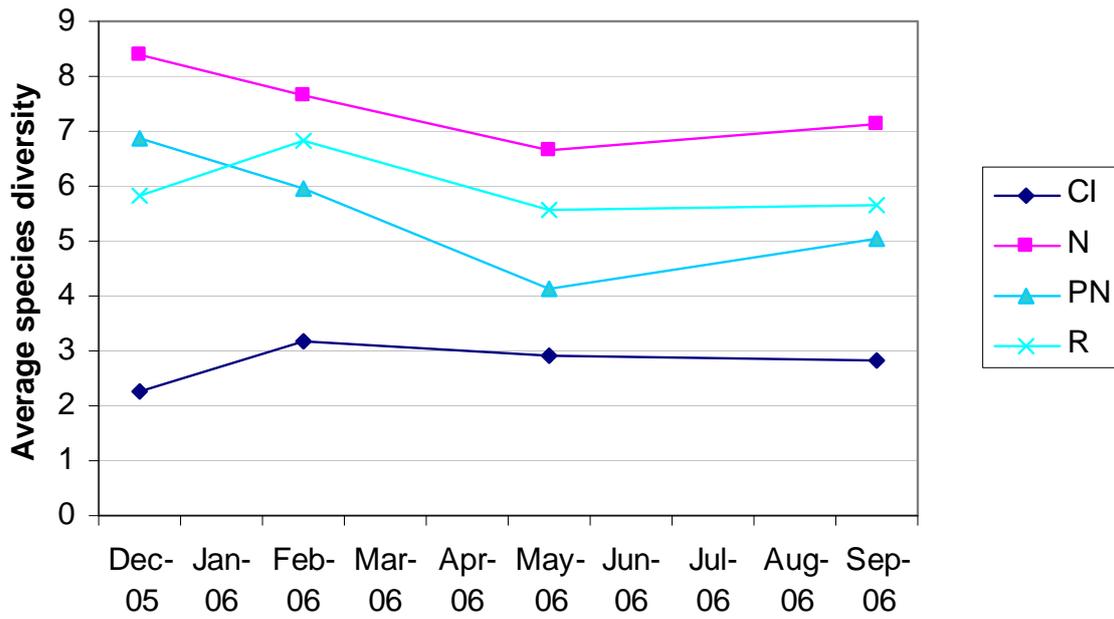


Fig. 18. Average number of ant species richness per sample during the sampling seasons (standard deviations in Table 2).

Table 2. Standard deviations ( $\pm$ ) of species richness per field type, during each of the four sampling seasons.

	Dec-05	Feb-06	May-06	Sep-06
CI	1.05	1.11	1.67	1.4
N	3.07	3.25	2.4	2.6
PN	2.27	2.31	1.6	1.95
R	2.2	1.99	1.5	3.33

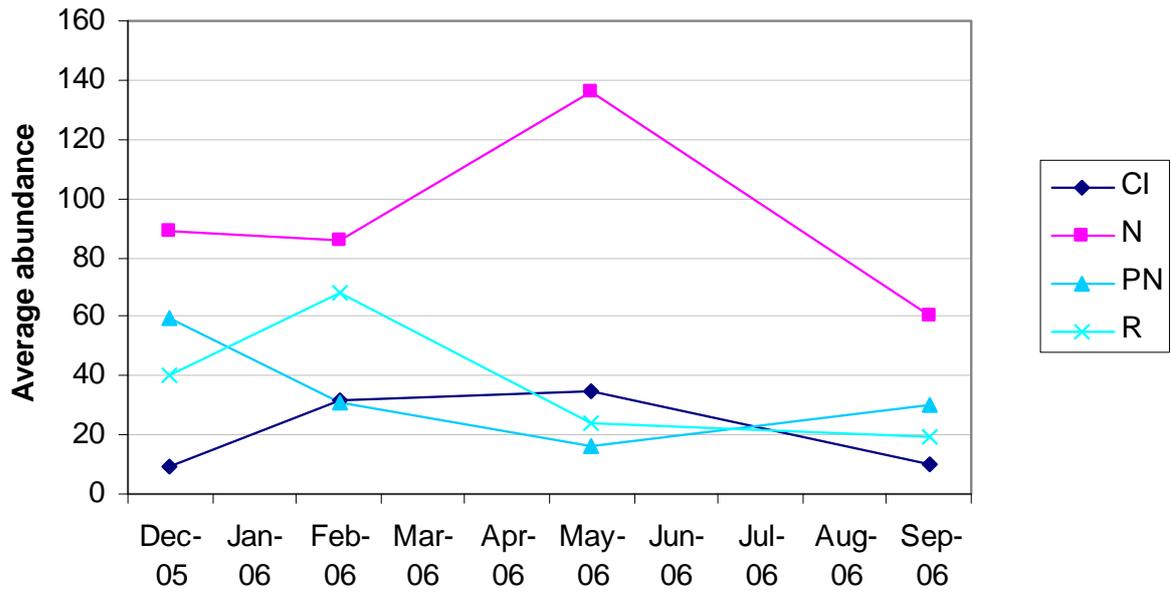


Fig. 19. Average ant abundances over the seasons (standard deviations in Table 3).

Table 3. Standard deviations ( $\pm$ ) of ant abundances during the sampling seasons

	Dec-05	Feb-06	May-06	Sep-06
CI	14.95	31.52	56.53	6.92
N	64.5	87.2	239.09	56.25
PN	43.29	17.46	12.72	29.77
R	25.8	40.12	15.54	12.59

### 3.2 DIFFERENCES BETWEEN ANT SPECIES ASSEMBLAGES

Analysis of Similarity (ANOSIM) was used to establish the significance of the differences between ant species assemblages that occurred in the four different habitat types described in section 2.2 (Site Selection). Multivariate ANOSIM gave the pairwise test comparisons between the four field types. The R-values gave a measure of the separateness of these groupings based on ant species assemblage (Clarke & Gorley, 2001). There was a significant difference between almost all of the ant species assemblages of the different field types ( $P < 0.05$ ) throughout all sampling times (December 2005 – September 2006). There were two exceptions however to this finding, i.e.; the ant species assemblages in the renosterveld (R) and fynbos invaded by pine (PN) were almost identical ( $R < 0.3$ ) during the February 2006 sampling catch; during May 2006, the undisturbed fynbos (N) and renosterveld (R) ant species assemblages were almost identical in species composition ( $R < 0.3$ ).

The greatest dissimilarity in ant species assemblages during the four sampling periods were between bluegum (CI) and undisturbed fynbos (N) sites ( $R > 0.7$ ) with almost no overlap in species composition between these areas.

According to the ANOSIM there seems to be a considerable overlap in species assemblage composition between uninvaded fynbos (N) and renosterveld (R) ( $R < 0.3$ ), as well as between these aforementioned groups and pine sites (P). In other words, there was great similarity between the species assemblages of the uninvaded fynbos, renosterveld and pine invaded sites. The R-values obtained with the SIMPER analysis (Table 4) indicate, that even though there is considerable “overlap” or “sharing” of species between clearly visibly different habitats (differences based on the dominant vegetation types), there is also enough “dissimilarity” to state that these field types or habitats harbour species assemblages adapted to the vegetation types occurring in these habitats.

This indicates that planting or invasion by pine tree is not critical for abundant species. It should be bourn in mind that neither ANOSIM nor SIMPER analysis are sensitive to rare species.

The natural fynbos sites yielded certain species unique to these undisturbed conditions (e.g.: *Camponotus* spp.), and the renosterveld sites also had species that preferred the conditions of these habitats (*Messor* spp. and *Crematogaster* spp.), which occur at lower abundances than some of the more common species (*Tetramorium* spp. and *Monomorium* spp.) which were sampled at high abundances in both disturbed and undisturbed habitats.

Cluster analysis of all summed data for all seasons revealed a clear grouping of species abundance according to the habitat type (Fig. 20). The first group which separated out (CI) included very shaded sites with high density of bluegum trees and shading of at least 80 %. These sites were also characterized by complete absence of indigenous vegetation. The rest of the sites all retained indigenous fynbos vegetation, but group together according to their distinct ant assemblages, which closely followed the distinctive vegetation types.

RE and RW represented grouped samples from renosterveld (R). The sampled ant assemblages from these sites were distinct from the other sites, with a higher abundance of arboreal ants there (*Crematogaster* spp.). PP, GZP and PMXD were fynbos sites invaded by pine trees (PN). These pines had a dense, shady canopy. Pri1, Pri2 and GZ were uninvaded natural sites where the greatest species richness was obtained per sampling point. Pri1 (uninvaded fynbos) was dissimilar to the remaining sites in terms of species assemblage, and can be considered unique, but was grouped in the ANOSIM analysis because of the area's similarity in vegetation type to the other natural areas. The CLUSTER (Fig. 20) supports the *a priori* grouping of sites and samples into distinct habitat types.

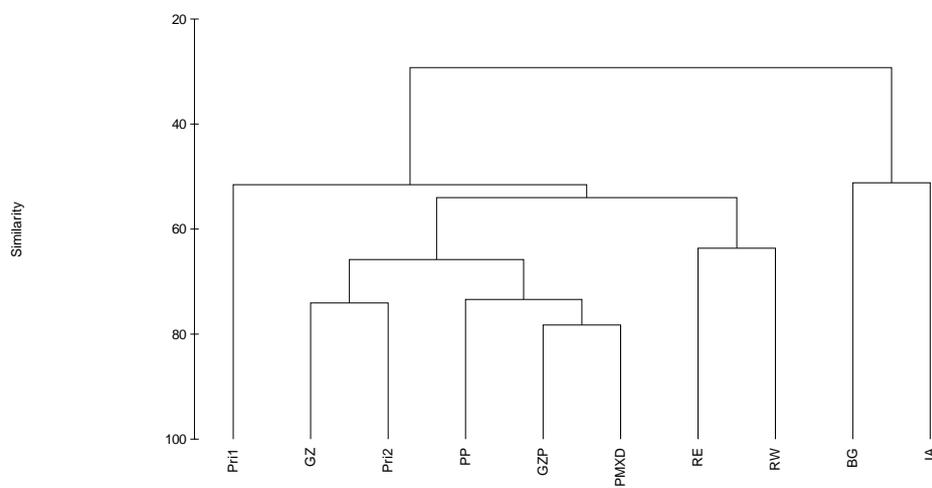
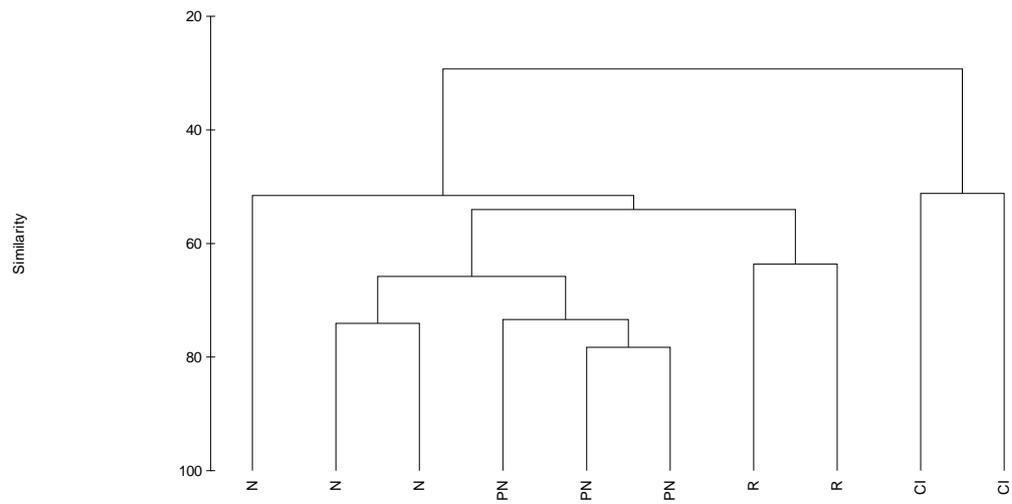


Fig. 20. CLUSTER dendrogram of ant species abundance data for all seasons combined. The dendrogram was derived from summed, fourth-root transformed data. Abbreviations in A represent specific sites, and in B, these site names are replaced with the vegetation types (section 2.2).

### 3.3 SPECIES ASSEMBLAGE PATTERNS DURING SAMPLING SEASONS

DCA was done for the December 2005, February 2006, May 2006 and September 2006 abundance data in order to measure the length of the first gradient and determine whether linear (RDA) or unimodal (CCA) gradient analysis methods should be undertaken. Gradient analysis yielded a 1<sup>st</sup> axis length for respective seasons: Dec-05: 4.385, Feb-06: 5.521, May-06: 4.802, and Sept-06: 4.535. The gradient lengths were all above 3.0, therefore, a unimodal gradient analysis, Canonical Correspondance Analysis (CCA) was undertaken to determine the impacts of the environmental variables (including Argentine ant per season) on the observed changes in assemblage structure during the separate sampling seasons (Lepš & Šmilauer, 2003).

Table. 4.

Characteristic species of Formicidae for each field type (dominant vegetation type) per season, using SIMPER analysis for species that cumulatively contributed over 90 % of the total abundance.

Dec-05	Jan-06	May-06	Sep-06
<b>Completely invaded (bluegum)</b>			
<i>Monomorium</i> sp. 8	<i>Linepithema humile</i>	<i>Linepithema humile</i>	<i>Tetramorium</i> sp. 1
<i>Tetramorium frigidum</i>	<i>Monomorium</i> sp. 8	<i>Monomorium</i> sp. 8	<i>Monomorium</i> sp. 8
<i>Linepithema humile</i>	<i>Tetramorium frigidum</i>	<i>Tetramorium</i> sp. 1	<i>Tetramorium frigidum</i>
<i>Tetramorium similum</i> -group	<i>Tetramorium</i> sp. 1		
<b>Natural fynbos</b>			
<i>Linepithema humile</i>	<i>Ocymyrmex barbiger</i>	<i>Ocymyrmex barbiger</i>	<i>Meranoplus</i> sp. 1
<i>Ocymyrmex barbiger</i>	<i>Ocymyrmex</i> sp. 2	<i>Linepithema humile</i>	<i>Linepithema humile</i>
<i>Meranoplus peringueyi</i>	<i>Linepithema humile</i>	<i>Tetramorium quadrispinosum</i>	<i>Tetramorium quadrispinosum</i>
<i>Tetramorium quadrispinosum</i>	<i>Tetramorium quadrispinosum</i>	<i>Meranoplus peringueyi</i>	<i>Monomorium</i> sp. 8
<i>Monomorium</i> sp. 15	<i>Meranoplus peringueyi</i>	<i>Monomorium</i> sp. 15	<i>Ocymyrmex barbiger</i>
<i>Camponotus</i> sp. 1	<i>Monomorium</i> sp. 15	<i>Camponotus</i> sp. 1	<i>Monomorium</i> sp. 15
<i>Plagiolepis</i> sp. 2	<i>Pheidole capensis</i>	<i>Ocymyrmex</i> sp. 2	<i>Camponotus</i> sp. 1
<i>Monomorium</i> sp. 8		<i>Lepisiota capensis</i>	<i>Camponotus</i> sp. 2
<b>Fynbos invaded by pine</b>			
<i>Meranoplus</i> sp. 1	<i>Linepithema humile</i>	<i>Linepithema humile</i>	<i>Meranoplus peringueyi</i>
<i>Linepithema humile</i>	<i>Ocymyrmex barbiger</i>	<i>Ocymyrmex barbiger</i>	<i>Linepithema humile</i>
<i>Ocymyrmex barbiger</i>	<i>Meranoplus peringueyi</i>	<i>Meranoplus peringueyi</i>	<i>Monomorium</i> sp. 8
<i>Monomorium</i> sp. 15	<i>Tetramorium quadrispinosum</i>	<i>Monomorium</i> sp. 8	<i>Tetramorium</i> sp. 2
<i>Tetramorium frigidum</i>	<i>Monomorium</i> sp. 8	<i>Tetramorium quadrispinosum</i>	<i>Tetramorium</i> sp. 1
<i>Tetramorium</i> sp. 2	<i>Monomorium</i> sp. 15	<i>Lepisiota capensis</i>	<i>Tetramorium frigidum</i>
<i>Monomorium</i> sp. 8	<i>Lepisiota capensis</i>		
<b>Renosterveld</b>			
<i>Tetramorium quadrispinosum</i>	<i>Tetramorium quadrispinosum</i>	<i>Tetramorium quadrispinosum</i>	<i>Tetramorium quadrispinosum</i>
<i>Tetramorium frigidum</i>	<i>Ocymyrmex barbiger</i>	<i>Linepithema humile</i>	<i>Monomorium</i> sp. 15
<i>Monomorium</i> sp. 15	<i>Linepithema humile</i>	<i>Ocymyrmex barbiger</i>	<i>Ocymyrmex barbiger</i>
<i>Ocymyrmex barbiger</i>	<i>Monomorium</i> sp. 15	<i>Tetramorium frigidum</i>	<i>Tetramorium frigidum</i>
<i>Linepithema humile</i>	<i>Tetramorium erectum</i>	<i>Monomorium</i> sp. 15	<i>Meranoplus peringueyi</i>
<i>Meranoplus peringueyi</i>	<i>Tetramorium frigidum</i>		<i>Linepithema humile</i>
	<i>Monomorium</i> sp. 8		<i>Tetramorium</i> sp. 2
			<i>Tetramorium</i> sp. 1

Table 5. Mean abundance and standard deviation ( $\pm$ ) per pitfall for ant species December 2005, occurring in respective field types.

		CI		N		PN		R							
		mean	sd( $\pm$ )	ave	sd( $\pm$ )	ave	sd( $\pm$ )	ave	sd( $\pm$ )						
Cerapachyinae	<i>Cerapachys</i> sp. 3	3.9	10.5	16.6	15.0	14.4	16.3	2.2	2.8						
	<i>Cerapachys wroughtoni</i>														
Dolichoderinae	<i>Linepithema humile</i>	3.9	10.5	16.6	15.0	14.4	16.3	2.2	2.8						
	<i>Technomyrmex pallipes</i>														
Dorylinae	<i>Dorylus helvolus</i>					0.4	0.8								
Formicinae	<i>Camponotus angusticeps</i>	0.1	0.3	0.3	0.7	0.1	0.2	0.1	0.3						
	<i>Camponotus irredux</i>														
	<i>Camponotus maculatus</i> -group														
	<i>Camponotus mystaceus</i> -group														
	<i>Camponotus niveosetosis</i>														
	<i>Camponotus</i> sp. 1														
	<i>Camponotus</i> sp. 2														
	<i>Camponotus</i> sp. 3														
	<i>Camponotus</i> sp. 4														
	<i>Camponotus</i> sp. 5														
	<i>Camponotus vestitus</i> -group														
	<i>Lepisiota capensis</i>														
	<i>Plagiolepis</i> sp. 1														
	<i>Plagiolepis</i> sp. 2														
<i>Plagiolepis</i> sp. 3															
Myrmicinae	<i>CreMATogaster peringueyi</i>	2.4	3.3	13.4	16.2	14.9	18.0	2.7	5.3						
	<i>Meranoplus peringueyi</i>							6.3	12.3						
	<i>Messor capensis</i>							3.4	10.3						
	<i>Monomorium</i> sp. 15							7.4	8.2						
	<i>Monomorium</i> sp. 8							0.4	0.8						
	<i>Ocymyrmex barbiger</i>							2.8	3.4						
	<i>Ocymyrmex</i> sp. 2														
	<i>Pheidole capensis</i>							0.3	1.2						
	<i>Pyramica</i> sp. 1														
	<i>Solenopsis</i> sp. 1							0.1	0.2						
	<i>Solenopsis</i> sp. 2														
	<i>Solenopsis</i> sp. 3							0.1	0.2						
	<i>Tetramorium erectum</i>							0.1	0.3	0.4	1.0	0.1	0.3		
	<i>Tetramorium quadrispinosum</i>							8.9	8.4	3.6	8.2	10.9	8.8		
	<i>Tetramorium</i> sp. 1							0.6	1.2	0.6	1.6	0.8	2.0	0.3	0.9
	<i>Tetramorium</i> sp. 2							0.1	0.3	0.2	0.5	2.9	5.1	0.8	1.4
	<i>Tetramorium similum</i> -group							0.5	1.2					0.5	1.2
	<i>Tetramorium</i> sp. 4									0.3	0.8	0.3	1.2		
	<i>Tetramorium frigidum</i>							1.9	2.9	0.6	1.1	2.0	2.4	2.3	2.1
	<i>Tetramorium</i> sp. 6											0.3	1.2		
Total number of ants								3269							

Table 6. Summary of Eigenvalues and Monte Carlo test for the CCA ordination diagram of December 2006 ant abundance data.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.392	0.202	0.099	0.085	3.515
Species-environment correlations	0.903	0.849	0.733	0.576	
Cumulative percentage variance					
of species data	11.1	16.9	19.7	22.1	
of species-environment relation	43.6	66.1	77.1	86.5	
Monte Carlo test of significance	F-ratio	P-value			
First canonical axis (eigenvalue = 0.392)	6.525	0.002			
All canonical axis (Trace = 0.899)	2.553	0.02			

Table 7. Conditional effects from direct gradient analysis methods showing the environmental variables in descending order of influence on species abundance during December 2005.

Variable	Var.N	P	F
naturaln	1	0.002	6.78
Vegetati	5	0.002	3.08
Lin hum	7	0.012	2.22
elevatio	4	0.016	1.68
l.l.cove	3	0.1	1.48
shading	6	0.358	1.06
l.l.dept	2	0.476	0.86

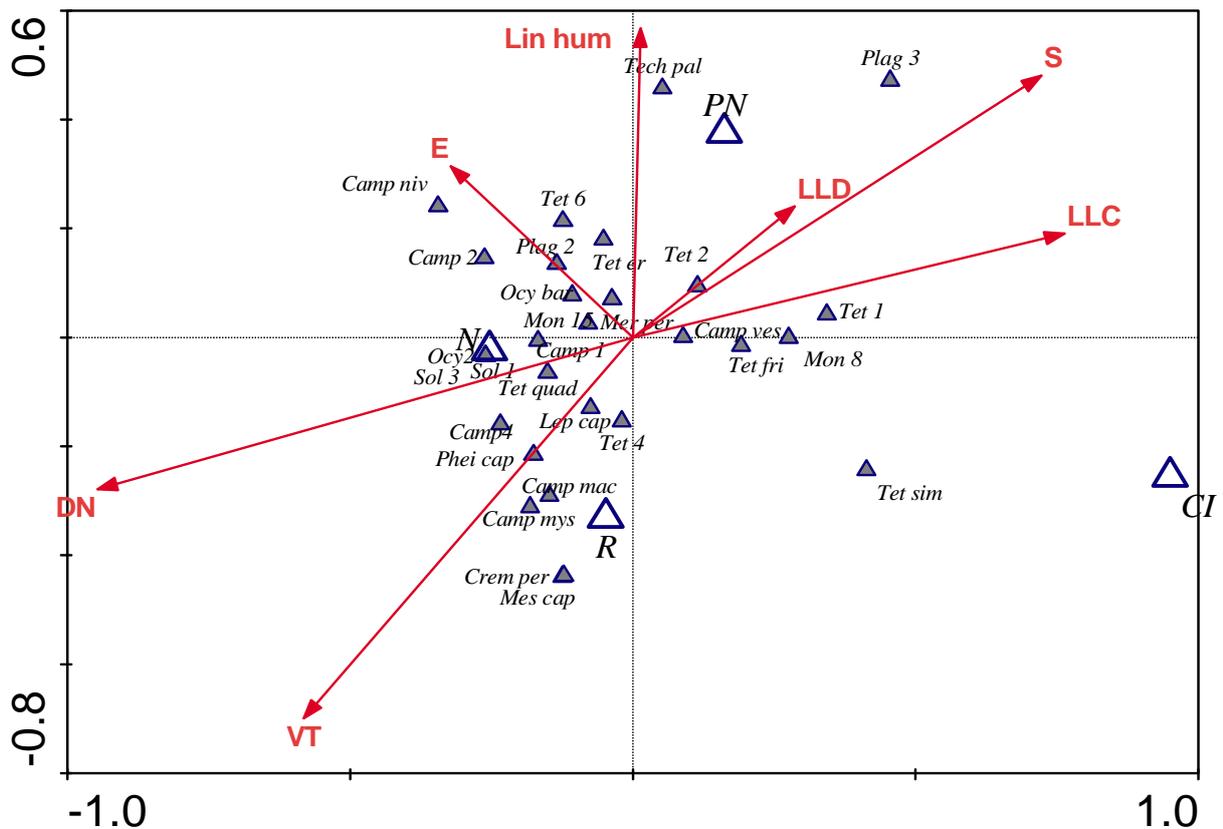


Fig 21. CCA of environmental variables affecting ant distribution patterns across the sampled areas during the December 2005 sampling period. Dummy variables (PN, CI, R and N) represent the dominant vegetation types (see section 2.2). Abbreviated species names with their full names can be found in Appendix A. VT: vegetation type, DN: degree of naturalness, E: elevation, S: shading, LLD: leaf litter depth, LLC: leaf litter cover.

### 3.3.1 Assemblage patterns during the December 2005 sampling period

During December, the species favouring natural sites are separated by the vertical axis from those species that prefer disturbed (PN and CI) habitats. Leaf litter cover is greatest in the invaded sites, whilst shading is also important (Fig. 21). SIMPER analysis (Table 4) shows that *Monomorium* sp. 8, *Tetramorium frigidum*, *Linepithema humile* and *Tetramorium similum*-group were characteristic of the bluegum sites (CI). *Tetramorium* sp. 1 and *Plagiolepis* sp. 3 and *Camponotus vestitus*-group (Table 5) did not appear in the

SIMPER analysis as they occurred in low numbers, but the ordination diagram (Fig. 21) clearly shows that they occurred predominantly in areas invaded by bluegum or pine trees.

*Technomyrmex pallipes* and *Tetramorium* sp. 6 were species that occurred only in old fynbos sites invaded by pine trees (Table 5). These sites differed from natural sites in having upper canopy shading, and leaf litter layer distinct from the scattered organic material associated with fynbos ground layers. The bluegum sites had species assemblages radically different from all the other sites, with very low species richness consisting of *Monomorium* sp. 8, *Tetramorium* sp. 1 and *T. frigidum*.

The ordination diagram (Fig. 21) shows that most *Camponotus* spp. generally occurred in natural uninvaded fynbos sites, where the natural vegetation type predominated. SIMPER analysis (Table 4) however shows that the number of species shared between undisturbed and disturbed fynbos is large, as they share five species characteristic of the group, with the natural fynbos having three species characteristic of these areas not occurring in sites invaded by pine and bluegum trees.

*Tetramorium quadrispinosum*, *Plagiolepis* sp. 1, and including all the *Camponotus* spp. sampled in December 2006 are characteristic of natural fynbos sites occurring at high abundances throughout the sampled areas (N-sites). These natural vegetation types were distinguishable from invasive vegetation type habitats by a relatively low layer of fynbos plant cover over a soil surface that was bare but for some dead scattered organic material used by the local ants for the construction of nest mounds. *Camponotus maculatus*-group, *Camponotus mystaceus*-group, *Crematogaster peringueyi* and *Messor capensis* lie close to 'R' (renosterveld sites) in the ordination diagram (Fig. 21) indicating a preference for this habitat type.

Both Monte Carlo tests for the CCA on the 1st and all axes were highly significant ( $P = 0.002$ ) (Table 6). Species assemblages are clearly sensitive to the environmental variables as used in the analysis. Conditional effects (Table 7) show that degree of naturalness ( $P = 0.002$ ,  $F = 6.78$ ), vegetation type ( $P = 0.002$ ,  $F = 3.08$ ), *L. humile* abundance ( $P = 0.012$ ,  $F = 2.22$ ) and elevation ( $P = 0.016$ ,  $F = 1.68$ ) were highly significant in affecting species distribution patterns across the landscape.

These results are supported by Spearman's Correlation Coefficient which yielded a positive statistically significant correlation of the degree of naturalness with a large number of ant species. The majority of these ants preferred relatively pristine fynbos habitat. These species include nearly all *Camponotus* spp. sampled in December 2005 ( $P < 0.05$ ,  $R > 0.29$ ) with the exception of *C. vestitus*-group and *Camponotus niveosetosus*. Other ant significantly attracted to natural area types are *Crematogaster peringueyi*, *Meranoplus peringueyi*, *M. capensis*, *Monomorium* sp. 15, *Ocymyrmex barbiger*, *Pheidole capensis*, *Plagiolepis* sp. 2 and *T. quadrispinosum*.

Species that correlated positively and significantly with vegetation type ( $P < 0.05$ ,  $R > 0.26$ ) were *C. maculatus*-group, *C. mystaceus*-group, *C. peringueyi* and *T. quadrispinosum*: all of these are species that occur at very high abundances at sampling points that were placed in pristine low-growing fynbos vegetation. Conversely there was a negative regression with *T. pallipes* and *Tetramorium* sp. 2 ( $P < 0.05$ ,  $R < -0.28$ ).

*L. humile* abundance showed statistically significant negative correlations ( $P < 0.05$ ,  $R < -0.27$ ) with *C. peringueyi*, *Lepisiota capensis*, *M. capensis* and *T. similum*-group. However, there was a positive correlation with *Monomorium* sp. 8 and *O. barbiger* ( $P < 0.05$ ,  $R > 0.27$ ).

Elevation shows a statistically significant negative correlation with *L. capensis* ( $P < 0.05$ ,  $R = -0.26$ ) and a positive correlation with *L. humile* ( $P < 0.05$ ,  $R = 0.35$ ).

The other environmental variables had little impact on species assemblages according to the analysis done for December 2005 data, or rather, the indigenous ant communities as a whole did not respond sufficiently to the changes associated with shading, leaf litter depth, and leaf litter cover (Table 7) during that particular season.

Table 8. Mean abundance and standard deviation ( $\pm$ ) per pitfall for ant species during February 2006, occurring in respective field types.

		CI		N		PN		R	
		mean	sd( $\pm$ )						
Cerapachyinae	<i>Cerapachys</i> sp. 3							0.1	0.3
	<i>Cerapachys wroughtoni</i>								
Dolichoderinae	<i>Linepithema humile</i>	23.7	27.7	29.6	72.5	8.0	7.4	12.3	17.0
	<i>Technomyrmex pallipes</i>								
Dorylinae	<i>Dorylus helvolus</i>					0.1	0.2		
Formicinae	<i>Camponotus angusticeps</i>			0.3	1.0				
	<i>Camponotus irredux</i>			0.1	0.2				
	<i>Camponotus maculatus</i> -group			0.3	0.6				
	<i>Camponotus mystaceus</i> -group			1.7	3.3				
	<i>Camponotus niveosetosis</i>			0.2	0.5			0.1	0.3
	<i>Camponotus</i> sp. 1			0.3	0.5	0.1	0.3		
	<i>Camponotus</i> sp. 2			0.2	0.7				
	<i>Camponotus</i> sp. 3								
	<i>Camponotus</i> sp. 4								
	<i>Camponotus</i> sp. 5								
	<i>Camponotus vestitus</i> -group			0.5	1.2	0.2	0.4	0.1	0.3
	<i>Lepisiota capensis</i>	0.3	0.9	2.8	5.7	2.5	3.7	5.5	12.4
	<i>Plagiolepis</i> sp. 1			0.1	0.2				
	<i>Plagiolepis</i> sp. 2			0.2	0.5			0.1	0.3
	<i>Plagiolepis</i> sp. 3			0.3	0.6				
Myrmicinae	<i>Crematogaster peringueyi</i>							7.7	19.6
	<i>Meranoplus peringueyi</i> 1			4.1	5.6	3.1	4.0	8.8	25.5
	<i>Messor capensis</i>					0.1	0.2	1.5	3.5
	<i>Monomorium</i> sp. 15			1.2	2.0	1.6	2.5	8.8	11.1
	<i>Monomorium</i> sp. 8	1.9	2.5	0.3	0.6	1.4	2.1	0.5	0.8
	<i>Ocymyrmex barbiger</i>			13.9	12.4	4.8	4.7	6.6	5.9
	<i>Ocymyrmex</i> sp. 2			5.7	5.5	0.5	1.1	1.2	2.3
	<i>Pheidole capensis</i>			14.8	26.7	0.1	0.2		
	<i>Pyramica</i> sp. 1			0.1	0.2				
	<i>Solenopsis</i> sp. 1	0.1	0.3	0.2	0.7	0.2	0.5		
	<i>Solenopsis</i> sp. 2			0.1	0.2				
	<i>Solenopsis</i> sp. 3								
	<i>Tetramorium erectum</i>			0.3	0.8	0.6	1.5	1.1	1.8
	<i>Tetramorium quadrispinosum</i>			8.4	10.9	5.7	9.4	10.8	8.9
	<i>Tetramorium</i> sp. 1	2.1	3.3	0.2	0.5	0.5	0.9	0.6	1.7
	<i>Tetramorium</i> sp. 2			0.2	0.9	0.3	1.0	0.2	0.4
	<i>Tetramorium similum</i> -group							0.1	0.3
	<i>Tetramorium</i> sp. 4							0.1	0.3
	<i>Tetramorium frigidum</i>	3.3	4.2	0.1	0.2	1.1	2.8	1.6	2.0
	<i>Tetramorium</i> sp. 6	0.4	1.4					0.3	1.2

Total number of ants

3290

Table 9. Summary of Eigenvalues and Monte Carlo test for the CCA ordination diagram of February 2006 abundance data.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.485	0.191	0.087	0.075	4.038
Species-environment correlations	0.936	0.847	0.695	0.551	
Cumulative percentage variance					
of species data	12	16.7	18.9	20.7	
of species-environment relation	51.5	71.7	81	88.9	
Monte Carlo test of significance	F-ratio	P value			
First canonical axis (eigenvalue = 0.485)	7.1	0.002			
All canonical axes (Trace = 0.942)	2.262	0.002			

Table 10. Conditional effects from direct gradient analysis methods, showing the environmental variables in descending order, which influenced species abundance for the February 2006 data.

Variable	Var.N	P	F
naturaln	1	0.002	7.79
Vegetati	5	0.002	2.4
elevatio	4	0.004	2.02
l.l.cove	3	0.188	1.26
shading	6	0.332	1.09
Lin hum	7	0.706	0.58
l.l.dept	2	0.76	0.51



changes caused by pine tree invasion. SIMPER analysis (Table 4) shows that for both field types, high abundances of *L. humile*, *O. barbiger*, *T. quadrispinosum*, *M. peringueyi*, and *Monomorium* sp. 15 are the most abundant species characteristic of both these areas. These areas have young pine trees, which do not seem to impact so heavily on the undercover fynbos vegetation. In sites where pine infestation was more severe, with older more mature trees, the Argentine ant is one of the dominant species of this site, occurring there at very high abundances.

The ordination diagram (Fig. 22) illustrates that the structure of certain assemblages varies greatly according to vegetation type. These species included the rarer ants found predominantly in fynbos and renosterveld areas (Table 8). *Camponotus angusticeps*, *P. capensis*, and other *Camponotus* spp. (Fig. 22) seem to respond more to vegetation type than degree of naturalness, even though the effects of naturalness do still play a part.

*Cerapachys wroughtoni* and *C. peringueyi* occurred only in the renosterveld sites. *Camponotus irredux* and *Pyramica* sp. 1 were highly localized, found only in one sampling point at higher elevations of fynbos (Fig. 22). Ordination results, like those in the SIMPER (Table 4), indicate that *T. frigidum* and *Tetramorium* sp. 1. (species of smaller, less robust body size) occurred predominantly in the alien tree invaded areas (Fig. 22).

Both Monte Carlo tests for the CCA on the 1<sup>st</sup> and on all axes were highly significant ( $P = 0.002$ ) (Table 9). Species assemblages are structured according to the environmental variables used in the analysis. Conditional effects (Table 10) show that degree of naturalness ( $P = 0.002$ ,  $F = 7.79$ ), vegetation type ( $P = 0.002$ ,  $F = 2.4$ ) and elevation ( $P = 0.004$ ,  $F = 2.02$ ) are highly significant in affecting species distribution patterns across the landscape. Leaf litter cover, shading, *L. humile* abundance and leaf litter depth do not have a significant impact on indigenous ant species assemblage distribution during this season.

The results for Spearman's Correlation Coefficient generally support the ordination diagram. Naturalness was significantly positively correlated with *C. maculatus*-group, *C. niveosetosis*, *Camponotus* sp. 1, *C. vestitus*-group ( $P < 0.05$ ,  $R > 0.28$ ), and with *C. peringueyi*, *M. peringueyi*, *Ocymyrmex* sp. 2, *P. capensis*, *Plagiolepis* sp. 1 and *T.*

*quadrispinosum* ( $P < 0.05$ ,  $R > 0.26$ ). *Ocymyrmex* spp. was the most highly positively correlated with degree of naturalness ( $R = 0.72$ ).

*Monomorium* sp. 8, *Tetramorium* sp. 1 and *T. frigidum* was significantly negatively correlated with naturalness ( $P < 0.05$ ,  $R < -0.31$ ). SIMPER analysis showed that the aforementioned species were characteristic of completely invaded sites (Table 4).

Vegetation type correlated positively and significantly with *C. maculatus*-group, *C. mystaceus*-group and *C. niveosetosis*, *Plagiolepis* sp. 3, *T. quadrispinosum* and *O. barbiger* ( $P < 0.05$ ,  $R > 0.28$ ). However, there was a negative correlation with *Monomorium* sp. 8 and *Tetramorium* sp. 1 ( $P < 0.05$ ,  $R < -0.26$ ), both species of small size, that may display submissive behaviour towards the larger, more robust ants.

Elevation correlated positively only with *L. humile* and *Plagiolepis* sp. 2 ( $P < 0.05$ ,  $R > 0.27$ ).

Abundances of the alien ant, *L. humile*, did not have a significant affect on indigenous ant communities according to the Monte Carlo test for significance (Table 10), despite its abundance (Table 4). This is a highly unusual result, as the species list (Table 8) clearly shows that Argentine ant abundance was particularly high, and that there were far higher abundances in the natural than in the invaded sites.

Table 11. Mean abundance and standard deviation ( $\pm$ ) per pitfall for ant species for May 2006, occurring in respective field types.

		CI		N		PN		R	
		mean	sd( $\pm$ )						
Cerapachyinae	<i>Cerapachys</i> sp. 3			0.1	0.5				
	<i>Cerapachys wroughtoni</i>								
Dolichoderinae	<i>Linepithema humile</i>	24.5	53.9	11.1	16.3	2.9	3.3	5.3	4.5
	<i>Technomyrmex pallipes</i>			0.1	0.2			1.3	3.4
Dorylinae	<i>Dorylus helvolus</i>								
Formicinae	<i>Camponotus angusticeps</i>								
	<i>Camponotus irredux</i>								
	<i>Camponotus maculatus</i> -group			0.1	0.3				
	<i>Camponotus mystaceus</i> -group			2.9	7.3				
	<i>Camponotus niveosetosis</i>	0.1	0.3	0.2	0.4				
	<i>Camponotus</i> sp. 1			0.6	0.9				
	<i>Camponotus</i> sp. 2			0.2	0.7				
	<i>Camponotus</i> sp. 3								
	<i>Camponotus</i> sp. 4								
	<i>Camponotus</i> sp. 5							0.1	0.3
	<i>Camponotus vestitus</i> -group								
	<i>Lepisiota capensis</i>			8.4	15.7	0.9	1.6	0.9	3.2
	<i>Plagiolepis</i> sp. 1			0.2	0.7				
	<i>Plagiolepis</i> sp. 2	0.1	0.3	0.1	0.3			0.1	0.3
	<i>Plagiolepis</i> sp. 3			1.4	3.1	0.1	0.2		
Myrmicinae	<i>Crematogaster peringueyi</i>							2.3	6.9
	<i>Meranoplus peringueyi</i>			6.1	10.7	4.7	11.2	0.4	0.9
	<i>Messor capensis</i>					0.1	0.2	0.8	1.8
	<i>Monomorium</i> sp. 15			2.6	3.6	0.8	1.9	1.7	4.3
	<i>Monomorium</i> sp. 8	4.1	6.7	2.2	5.5	1.2	1.6	0.2	0.4
	<i>Ocymyrmex barbiger</i>			10.9	15.9	2.4	3.8	2.3	2.3
	<i>Ocymyrmex</i> sp. 2			1.8	3.6				
	<i>Pheidole capensis</i>			80.8	227.5				
	<i>Pyramica</i> sp. 1								
	<i>Solenopsis</i> sp. 1					0.1	0.2	0.1	0.3
	<i>Solenopsis</i> sp. 2	0.5	1.2	0.1	0.3			0.4	0.9
	<i>Solenopsis</i> sp. 3								
	<i>Tetramorium erectum</i>					0.1	0.2	0.2	0.6
	<i>Tetramorium quadrispinosum</i>			4.3	4.1	1.8	3.0	6.8	5.2
	<i>Tetramorium</i> sp. 1	3.4	4.5	0.2	0.4	0.2	0.4	0.2	0.4
	<i>Tetramorium</i> sp. 2	0.3	0.5	1.8	7.8	0.1	0.3	0.2	0.4
	<i>Tetramorium similum</i> -group	0.1	0.3						
	<i>Tetramorium</i> sp. 4								
	<i>Tetramorium frigidum</i>	1.9	3.6	0.1	0.3	0.9	2.0	0.9	1.2
	<i>Tetramorium</i> sp. 6							0.4	1.4
Total number of ants									3455

Table 12. Summary of Eigenvalues and Monte Carlo test for the CCA ordination diagram of May 2006 abundance data.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.445	0.218	0.196	0.115	4.734
Species-environment correlations :	0.902	0.842	0.837	0.677	
Cumulative percentage variance					
of species data :	9.4	14	18.1	20.6	
of species-environment relation:	40	59.6	77.3	87.6	
Monte Carlo test of significance:	F-ratio	P-value			
First canonical axis (eigenvalue = 0.445)	5.394	0.002			
All canonical axes (Trace = 1.111)	2.277	0.002			

Table 13. Conditional effects fro direct gradient analysis, showing the environmental variable in descending order, which influenced species abundance for the May 2006 data.

Variable	Var.N	P	F
naturaln	1	0.002	5.9
Lin hum	7	0.032	2.61
Vegetati	5	0.002	2.38
elevatio	4	0.004	2.27
l.l.cove	3	0.508	0.93
shading	6	0.628	0.92
l.l.dept	2	0.776	0.48

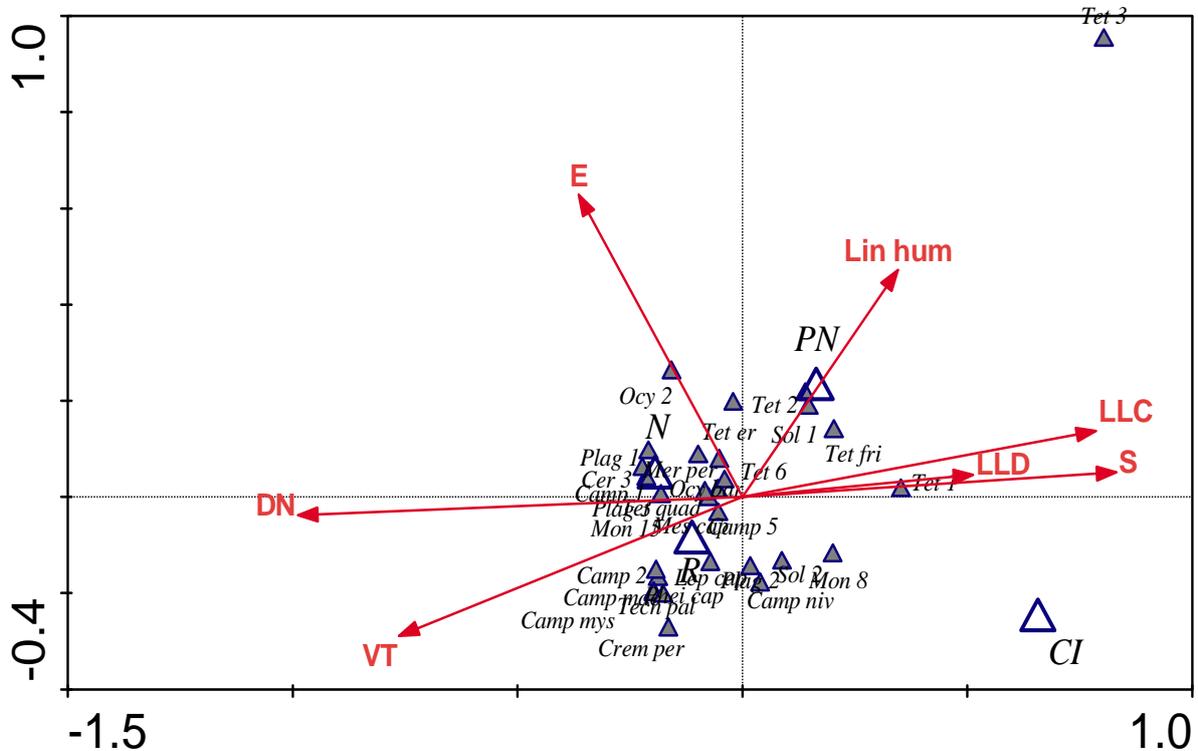


Fig 23. CCA of environmental variables affecting ant distribution patterns across the sampled areas during the May 2006 sampling period. Dummy variables (PN, CI, R and N) represent the dominant vegetation types (see section 2.2). Abbreviated species names with their full names can be found in Appendix A. VT: vegetation type, DN: degree of naturalness, E: elevation, S: shading, LLD: leaf litter depth, LLC: leaf litter cover.

### 3.3.3 Assemblage patterns during the May 2006 sampling period

Ants were most abundant during the May 2006 sampling season in the natural samples, possibly indicating that there were more species in the natural sites that are adapted to the onset of colder weather, but generally for all sites, the bluegum (CI) sites showed the lowest species richness (Fig. 18). According to the ANOSIM there was no dissimilarity between the natural fynbos, pine and renosterveld habitat sites. The ordination diagram (Fig. 23) illustrates the separation of species in groups that prefer natural habitats (left

axis) and those that occur in invaded sites (right axis). There is a very close association between fynbos areas invaded by pine and *L. humile* as an environmental variable.

Ants that co-occurred with *L. humile* at higher abundances were *Tetramorium* sp. 2 and *Solenopsis* sp. 1. Species that occurred predominantly in fynbos and renosterveld sites (Table 11) cluster strongly as a result of vegetation type in the ordination diagram (Fig. 23). This trend is similar to that found in February 2006.

SIMPER analysis (Table 4) showed that *L. humile*, *Monomorium* sp. 8 and *Tetramorium* sp. 1 are species characteristic of habitats invaded by bluegum trees. This trend is also seen in the ordination diagram (Fig. 23). Fynbos habitats invaded by pine trees shared five characteristic species.

Species that occurred at low abundances showed a greater specificity for certain habitat types, primarily in the natural fynbos sites. Many of the *Camponotus* species sampled occurred only in natural habitats (Table 11). *M. capensis* and *C. peringueyi* occurred at high abundances in renosterveld habitats, and at lower abundances in sites invaded by pine trees. Other species, predominantly of the Myrmicinae showed less specificity to habitat type (Table 11).

Both Monte Carlo tests for the CCA on the 1<sup>st</sup> and on all axes were highly significant ( $P = 0.002$ ) (Table 12). Species assemblages are structured according to the environmental variables used in the analysis. Conditional effects (Table 13) show that degree of naturalness ( $P = 0.002$ ,  $F = 5.9$ ), *L. humile* abundance ( $P = 0.032$ ,  $F = 2.61$ ), vegetation type ( $P = 0.002$ ,  $F = 2.38$ ) and elevation ( $P = 0.004$ ,  $F = 2.27$ ) were highly significant in affecting species distribution patterns across the landscape. Leaf litter cover, shading, and leaf litter depth did not have a significant affect on indigenous ant species assemblages using CCA during the analysis for this season.

The results for Spearman's Correlation Coefficient generally support the trends illustrated on the ordination diagram (Fig. 23) Degree of naturalness correlated significantly and positively with *Camponotus* sp. 1, *C. mystaceus*-group, *C. peringueyi*, *M. peringueyi*, *Monomorium* sp. 15, *O. barbiger*, *Ocymyrmex* sp. 2, *P. capensis*, *Plagiolepis* sp. 3, *T.*

*pallipes*, and *T. quadrispinosum* ( $P < 0.05$ ,  $R > 0.25$ ), while it correlated negatively with *Tetramorium* sp. 1 ( $P < 0.05$ ,  $R = -0.33$ ).

*L. humile* abundance correlated negatively with *C. mystaceus*-group, *L. capensis* and *P. capensis* ( $P < 0.05$ ,  $R < -0.33$ ) and correlated positively with *Ocymyrmex* sp. 2 and *Tetramorium* sp. 1 ( $P < 0.05$ ,  $R > 0.28$ ).

Vegetation type correlated positively with *C. mystaceus*-group, *Camponotus* sp. 1, *P. capensis*, *Plagiolepis* sp. 3, *T. pallipes* and *T. quadrispinosum* ( $P < 0.05$ ,  $R > 0.26$ ),

Elevation correlated positively with *O. barbiger* ( $P < 0.05$ ,  $R = 0.29$ ) and negatively with *L. capensis* and *Monomorium* sp. 8 ( $P < 0.05$ ,  $R < -0.26$ ).

Table 14. Average abundance and standard deviation ( $\pm$ ) per pitfall for ant species during September 2006, occurring in respective field types.

		CI		N		PN		R	
		mean	sd( $\pm$ )						
Cerapachyinae	<i>Cerapachys</i> sp. 3			0.1	0.2				
	<i>Cerapachys wroughtoni</i>								
Dolichoderinae	<i>Linepithema humile</i>	2.4	5.0	13.5	21.8	12.3	19.0	0.9	1.2
	<i>Technomyrmex pallipes</i>	0.1	0.3			0.1	0.5		
Dorylinae	<i>Dorylus helvolus</i>							0.2	0.4
Formicinae	<i>Camponotus angusticeps</i>								
	<i>Camponotus irredox</i>								
	<i>Camponotus maculatus</i> -group			0.1	0.3				
	<i>Camponotus mystaceus</i> -group			0.7	1.8				
	<i>Camponotus niveosetosis</i>	0.1	0.3	0.2	0.5				
	<i>Camponotus</i> sp. 1	0.1	0.3	0.7	0.8	0.2	0.7		
	<i>Camponotus</i> sp. 2			1.2	2.7				
	<i>Camponotus</i> sp. 3			0.1	0.2				
	<i>Camponotus</i> sp. 4								
	<i>Camponotus</i> sp. 5								
	<i>Camponotus vestitus</i> -group								
	<i>Lepisiota capensis</i>			1.6	3.6				
	<i>Plagiolepis</i> sp. 1			0.1	0.3			0.3	0.5
	<i>Plagiolepis</i> sp. 2								
	<i>Plagiolepis</i> sp. 3	0.1	0.3	1.2	3.7	0.1	0.2		
Myrmicinae	<i>Crematogaster peringueyi</i>							0.3	0.5
	<i>Meranoplus peringueyi</i>			6.2	6.9	9.4	14.4	3.3	4.6
	<i>Messor capensis</i>							0.2	0.4
	<i>Monomorium</i> sp. 15			2.7	4.5	0.7	1.1	3.0	3.7
	<i>Monomorium</i> sp. 8	2.0	2.4	2.4	4.4	1.2	1.7	0.2	0.4
	<i>Ocymyrmex barbiger</i>			1.7	2.2	0.9	2.0	2.1	2.6
	<i>Ocymyrmex</i> sp. 2			0.1	0.2				
	<i>Pheidole capensis</i>			19.5	51.1				
	<i>Pyramica</i> sp. 1								
	<i>Solenopsis</i> sp. 1			0.4	1.0			0.2	0.4
	<i>Solenopsis</i> sp. 2			0.7	2.3				
	<i>Solenopsis</i> sp. 3			0.4	1.0				
	<i>Tetramorium erectum</i>					0.1	0.3		
	<i>Tetramorium quadrispinosum</i>			6.4	7.3	0.8	1.4	2.2	1.4
	<i>Tetramorium</i> sp. 1	2.8	2.5	0.2	0.4	1.2	1.7	2.1	3.4
	<i>Tetramorium</i> sp. 2	0.1	0.3			1.8	2.7	2.0	2.7
<i>Tetramorium similum</i> -group			0.2	0.9			1.0	2.2	
<i>Tetramorium</i> sp. 4									
<i>Tetramorium frigidum</i>	2.4	2.9	0.3	0.6	1.2	1.7	1.4	1.7	
<i>Tetramorium</i> sp. 6									

Total number of ants

1980

Table 15. Summary of Eigenvalues and Monte Carlo test for the CCA ordination diagram of September 2006 abundance data.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.415	0.223	0.101	0.097	3.751
Species-environment correlations :	0.924	0.882	0.731	0.596	
Cumulative percentage variance					
of species data :	11.1	17	19.7	22.3	
of species-environment relation:	42.7	65.7	76.1	86.1	
Monte Carlo test of significance	F-ratio	P-value			
First canonical axis (eigenvalue = 0.415)	6.461	0.002			
All canonical axes (Trace = 0.971)	2.594	0.002			

Table 16. Conditional effects from direct gradient analysis, showing the environmental variables in descending order, which influence species abundance for the September 2006 data.

Variable	Var.N	P	F
naturaln	1	0.002	6.89
Vegetati	5	0.002	3.23
elevatio	4	0.008	2.15
l.l.cove	3	0.036	1.86
Lin hum	7	0.18	1.37
shading	6	0.16	1.33
l.l.dept	2	0.632	0.6

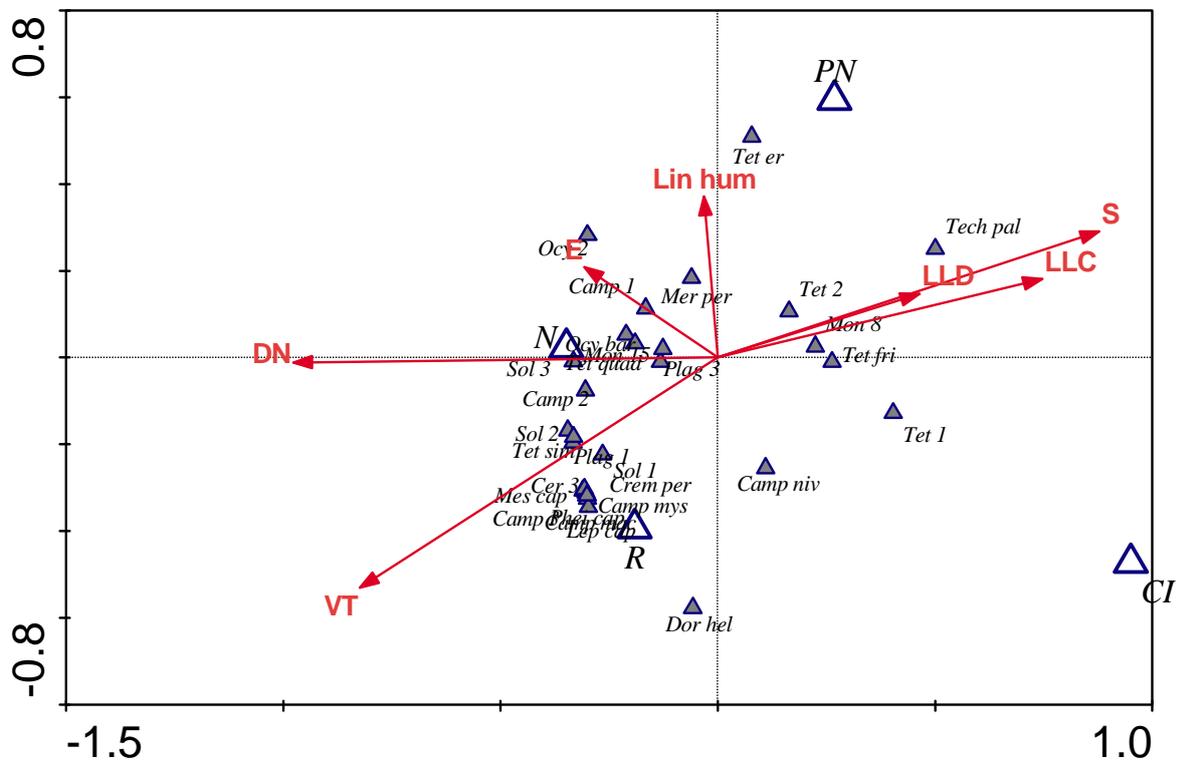


Fig. 24. CCA of environmental variables affecting ant distribution patterns across the sampled areas during the September 2006 sampling period. Dummy variables (PN, CI, R and N) represent the dominant vegetation types (see section 2.2). Abbreviated species names with their full names can be found in Appendix A. VT: vegetation type, DN: degree of naturalness, E: elevation, S: shading, LLD: leaf litter depth, LLC: leaf litter cover.

### 3.3.4 Assemblage patterns during the September 2006 sampling period

The ordination diagram (Fig. 24) shows a clumping of *C. maculatus*-group, *C. mystaceus*-group, *Camponotus* sp. 2, *Solenopsis* spp. and *P. capensis*, preferring the natural fynbos. Some of these species also occurred at lower abundances in sites invaded by pine trees. However, they clustered according to vegetation type (Fig. 24).

The species above the horizontal line on the right side of the vertical axis, such as *O. barbiger*, *Monomorium* sp. 15 and *T. quadrispinosum* all occurred in invaded sites, especially the areas invaded by pine trees. These species show a preference for the natural sites, as they occurred here in higher abundance.

Certain species may prefer the conditions caused by high woody plant aliens. These species include some *Tetramorium*, such as *Tetramorium erectum*, *Tetramorium* sp. 2 and *T. frigidum*. ANOSIM and SIMPER (Table 4) showed a greater dissimilarity in ant species assemblages between the natural fynbos and the pine infested fynbos sites, while there was greater similarity between pine and bluegum samples.

Both Monte Carlo tests for the CCA on the 1<sup>st</sup> and on all axes were highly significant ( $P = 0.002$ ) (Table 15). Species assemblages structured according to the environmental variables used in the analysis. Conditional effects (Table 16) show that degree of naturalness ( $P = 0.002$ ,  $F = 6.89$ ), vegetation type ( $P = 0.002$ ,  $F = 3.23$ ), elevation ( $P = 0.008$ ,  $F = 2.15$ ) and leaf litter cover ( $P = 0.036$ ,  $F = 1.86$ ) were highly significant in affecting species distribution patterns across the landscape. *L. humile* abundance, shading, and leaf litter depth did not have a significant affect on indigenous ant species assemblages according to CCA for data from this sampling time, but Spearman's Correlation Coefficient indicated that these environmental variables do have a high impact on individual species, but not on an entire assemblage *per se*.

The results for Spearman's Correlation Coefficient generally support the ordination diagram (Fig. 24). Naturalness correlated positively and significantly with *C. mystaceus*-group *Camponotus* sp. 1, *Camponotus* sp. 2, *C. peringueyi*, *L. capensis*, *M. peringueyi*, *Monomorium* sp. 15, *O. barbiger*, *P. capensis*, *Plagiolepis* sp. 1, *Solenopsis* sp. 3. *T. quadrispinosum* and *T. similum*-group ( $P < 0.05$ ,  $R > 0.26$ ), and correlated negatively with *Tetramorium* sp. 1 and *T. frigidum* ( $p < 0.05$ ,  $R < -0.31$ ) which were associated with invaded sites in the ordination diagram (Fig. 24).

*L. capensis*, *Monomorium* sp. 15, *O. barbiger*, *P. capensis*, *Plagiolepis* sp. 1, *Solenopsis* sp. 1, *T. quadrispinosum* and *T. similum*-group correlated positively and significantly with vegetation type ( $P < 0.05$ ,  $R > 0.26$ ).

*L. humile* and *Solenopsis* sp. 1 ( $P < 0.05$ ,  $R > 0.27$ ) correlated positively with elevation.

*Camponotus* sp. 1, *Camponotus* sp. 2, *L. capensis*, *Monomorium* sp. 15, *O. barbiger*, *P. capensis*, *Solenopsis* sp. 1, and *T. quadrispinosum* correlated significantly and negatively with leaf litter cover ( $P < 0.05$ ,  $R < -0.27$ ).

*L. humile* did not seem to affect assemblages during this sampling period according to the CCA.

Table 17. Summary of Eigenvalues and Monte Carlo test for CCA ordination diagram of pooled abundance data.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.395	0.164	0.069	0.047	5.03
Species-environment correlations :	0.897	0.791	0.513	0.51	
Cumulative percentage variance					
of species data :	7.8	11.1	12.5	13.4	
of species-environment relation:	54.4	77	86.5	93	
Monte Carlo test of significance:	F-ratio	P-value			
First canonical axis (eigenvalue = 0.395)	19.757	0.002			
All canonical axes (Trace = 0.726)	5.587	0.002			

Table 18. Conditional effects from direct gradient analysis, showing the environmental variables in descending order, which influence ant species abundances spatially.

Variable	Var.N	P	F
naturaln	1	0.002	19.75
Vegetati	5	0.002	6.61
elevatio	4	0.002	4.64
l.l.cove	3	0.002	2.56
shading	6	0.002	2.02
Linepith	7	0.192	1.33
l.l.dept	2	0.448	0.92

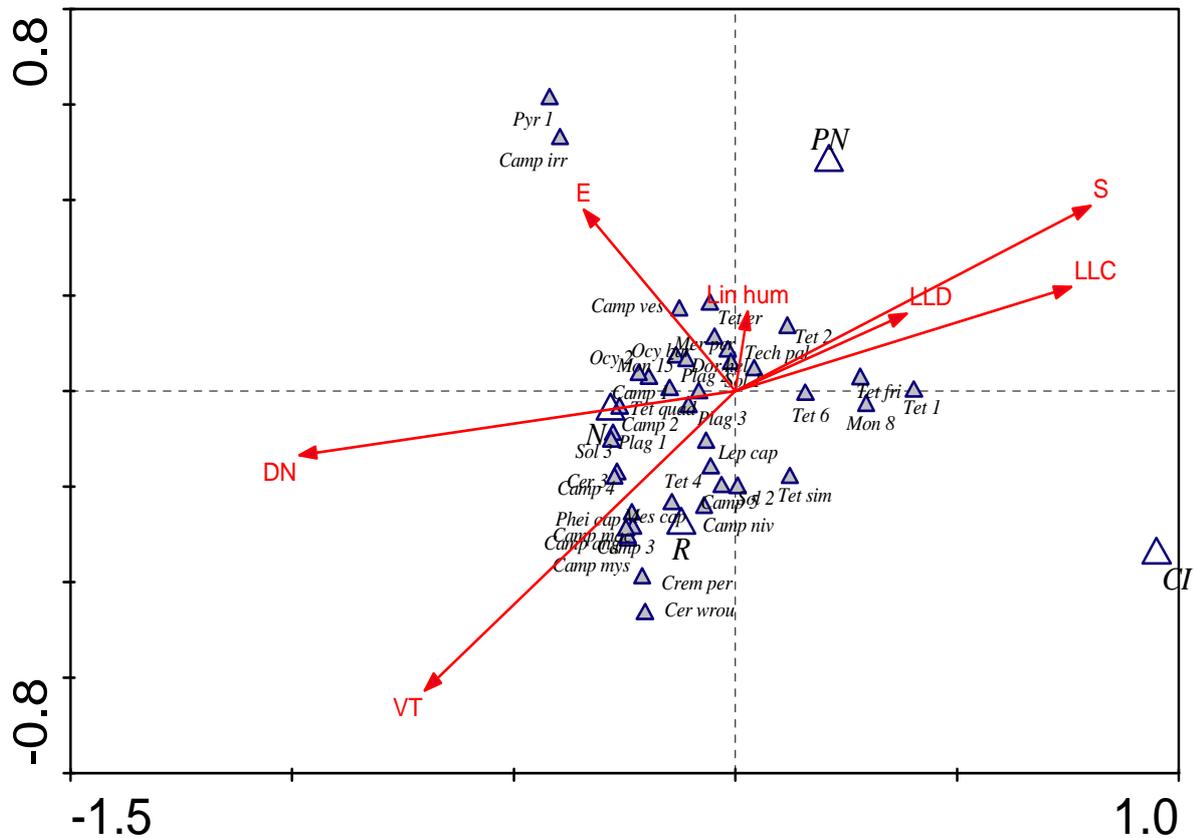


Fig. 25. CCA of environmental variables affecting ant species distribution patterns across the sampled areas, using pooled data from the entire sampling period (Dec-05 – Sept-06). Dummy variables (PN, CI, R and N) represent the dominant vegetation types (see section 2.2). Abbreviated species names with their full names can be found in Appendix A. VT: vegetation type, DN: degree of naturalness, E: elevation, S: shading, LLD: leaf litter depth, LLC: leaf litter cover.

### 3.4 ASSEMBLAGE PATTERNS DURING THE ENTIRE SAMPLING PERIOD (DEC-05 – SEPT-06) USING POOLED DATA

Both Monte Carlo tests for the CCA on the 1<sup>st</sup> and on all axes were highly significant ( $P = 0.002$ ) (Table 17). Species assemblages structured according to the environmental variables used in the analysis. Conditional effects (Table 18) show that degree of naturalness ( $P = 0.002$ ,  $F = 19.75$ ), vegetation type ( $P = 0.002$ ,  $F = 6.61$ ), elevation ( $P = 0.002$ ,  $F = 4.64$ ) and leaf litter cover ( $P = 0.002$ ,  $F = 2.56$ ), and shading ( $P = 0.002$ ,  $F = 2.02$ ) were highly significant in affecting species distribution patterns across the landscape. According to the CCA done on all data for the entire sample, *L. humile* abundance and leaf litter depth did not have a great impact on the structuring of the ant species assemblages.

The results for Spearman's Correlation Coefficient generally supported the ordination diagram (Fig. 25). Naturalness correlated positively and significantly with more than half of the species sampled throughout the study ( $P < 0.05$ ,  $R > 0.17$ ). The species that did not correlate with naturalness were species that occurred singly and rarely, such as *C. angusticeps*, *C. irredux*, *Camponotus* sp. 3, *C. wroughtoni* and *Cerapachys* sp. 3, *Pyramica* sp. 1, *Solenopsis* sp. 1 and *Solenopsis* sp. 2.

There was also no correlation with *T. pallipes*, *T. erectum*, *Tetramorium* sp. 2, *T. similum*-group, *T. frigidum* and *Tetramorium* sp. 6. These species are considered tramp species, and were not affected by the change in vegetation type that occurs with the progression of a plant invasion.

Naturalness correlated significantly and negatively with *Monomorium* sp. 8 and *Tetramorium* sp. 1 ( $P < 0.05$ ,  $R < -0.25$ ). These two species are very small and extreme generalists, which preferred the invaded sites because of the removal of possible competitors.

Vegetation type was significantly and positively correlated with *C. maculatus*-group, *C. mystaceus*-group, *C. niveosities*, *Camponotus* sp. 1, *C. peringueyi*, *M. capensis*, *Monomorium* sp. 15, *O. barbiger*, *Ocymyrmex* sp. 2, *P. capensis*, *Plagiolepis* sp. 1, *Plagiolepis* sp. 3, *Solenopsis* sp. 2, *T. quadrispinosum* and *T. similum*-group ( $P < 0.05$ ,  $R$

> 0.14). Vegetation type was negatively and significantly correlated with *Monomorium* sp. 8, *Teramorium* sp. 1 and *Tetramorium* sp. 2 ( $P < 0.05$ ,  $R < -0.16$ ), indicating that these species were not sensitive to change in vegetation structure.

Elevation correlated significantly and positively with *Monomorium* sp. 15, *O. barbiger*, *Solenopsis* sp. 1 and *T. quadrispinosum* ( $P < 0.05$ ,  $R > 0.15$ ), while it correlated negatively with *C. peringueyi*, *L. capensis* and *Monomorium* sp. 8 ( $P < 0.05$ ,  $R < -0.13$ ).

Leaf litter cover correlated positively and significantly with *Monomorium* sp. 8, *Tetramorium* sp. 1, *T. similum*-group and *T. frigidum* ( $P < 0.05$ ,  $R > 0.14$ ), while it correlated negatively and significantly with *C. maculatus*-group, *C. mystaceus*-group, *Camponotus* sp. 1, *Camponotus* sp. 2, *Camponotus* sp. 4, *L. capensis*, *Monomorium* sp. 15, *O. barbiger*, *Ocymyrmex* sp. 2, *P. capensis*, *Plagiolepis* sp. 2, *Solenopsis* sp. 3 and *T. quadrispinosum* ( $P < 0.05$ ,  $R < -0.14$ ).

Shading correlated positively and significantly with *Monomorium* sp. 8 and *Tetramorium* sp. 1 ( $P < 0.05$ ,  $R > 0.26$ ). It correlated negatively and significantly with *C. maculatus*-group, *C. mystaceus*-group, *C. niveosetosis*, *Camponotus* sp. 1, *Camponotus* sp. 2, *Camponotus* sp. 4, *C. peringueyi*, *L. capensis*, *M. peringueyi*, *M. capensis*, *Monomorium* sp. 15, *O. barbiger*, *Ocymyrmex* sp. 2, *P. capensis*, *Plagiolepis* sp. 1, *Plagiolepis* sp. 2, *Plagiolepis* sp. 3, and *T. quadrispinosum* ( $P < 0.05$ ,  $R < -0.13$ ).

Even though *L. humile* abundance was not a significant environmental variable for all samples done according to the CCA, Spearman's Correlation Coefficient showed that *L. humile* had a significant impact on certain endemic species; it correlated negatively with *C. mystaceus*-group, *C. peringueyi*, *L. capensis*, *M. capensis*, *P. capensis* and *T. similum*-group ( $P < 0.05$ ,  $R < -0.14$ ).

*L. humile* abundance correlated positively and significantly ( $P < 0.05$ ,  $R > 0.14$ ) with *C. vestitus*-group, *O. barbiger*, *Ocymyrmex* sp. 2, *Plagiolepis* sp. 3 and *T. quadrispinosum*.

CHAPTER 4  
DISCUSSION AND CONCLUSION

#### 4.1 EFFECTS OF INVASIVE PLANTS ON LOCAL ANT FAUNA

The effects of invasive plants such as *Pinus* and *Eucalyptus* (the two genera of woody plant that constituted the major invasive species on Vergelegen Estate), can be said to be deleterious for local endemic ants. These species form closed-canopy stands (Richardson & van Wilgen, 2004) which increase shading and bring in coolness into ecosystems. These two genera also produce 2 – 5 cm of packed leaf litter from pine and dry loose leaf litter from bluegum (Samways *et al.*, 2005). Overall, certain ants are highly sensitive to alien tree forests (Corley *et al.*, 2006).

This study found that the average ant abundances per season per sampling period showed that the natural fynbos sampling points (N-sites) yielded higher abundances and species richness of ants throughout the year than for invaded sites.

Indigenous ant abundance within invasive alien sites (i.e.: pine plantations) was significantly impoverished. Yet there were few differences in species richness of ants between invaded and uninvaded sites, but there were differences in both ant abundance and the composition of the ant assemblage, where ant abundances were much lower for invaded sites. Similar results have been obtained by Samways *et al.* (1996) and French and Major (2001) working on *Acacia* in fynbos. Moderate levels of invasiveness can in fact encourage certain species, but these are usually habitat generalists (Samways, 2005). A good example of such species found on Vergelegen Estate are *Tetramorium quadrispinosum*, *Meranoplus peringueyi* and *Monomorium* sp. 8, which were present in all sites, irrespective of the grade of woody plant and Argentine ant disturbance.

The results for this study show that pine and bluegum trees seriously compromise the integrity of local ant assemblages, by transforming the indigenous fynbos landscape.

A change in vegetation type affects native ants significantly. The species that correlated most with vegetation type (section 3.4) were also typical of uninvaded fynbos, and were also the most sensitive to change in vegetation type, especially wrought through a close canopy type vegetation, which affected epigaeic ants through changes in temperature, sunlight, and leaf litter cover to which these native ants are not adapted.

The severity of alien plant invasions has differential effects, and local ant assemblages may act and react according to their functional group adaptations (Agosti *et al.* 2000). A previous study by Corley *et al.* (2006) using similar methods employed in this study, showed that more open plantations resemble natural samples in a steppe biome. This study also shows that more open plantations (PN-sites) sustained ant assemblages which resembled those of the native fynbos samples. Open forest allows native under-storey vegetation to grow. In areas where alien trees (bluegum, the CI-sites) did not allow any under-storey growth, the ant assemblages were impoverished considerably. The only species that occurred here consistently but at low abundances were *Tetramorium* sp. 1, *Tetramorium frigidum* and *Monomorium* sp. 8.

The ordination diagram (fig. 25) shows that hot climate specialists (Agosti *et al.*, 2000) *Messor capensis*, *Meranoplus peringueyi* and *Ocymyrmex* spp. (Myrmecinae), did not occur in invaded sites, as the pine and bluegum trees decreased the amount of sunlight striking the soil surface (REF). These are seed harvester species that nest in the ground and prefer open relatively arid type habitats (Agosti *et al.*, 2000; Hölldobler & Wilson, 1990) that fynbos normally provides. The ordination diagram (fig. 25) showed that opportunists (Agosti *et al.*, 2000) such as *Technomyrmex pallipes* and *Tetramorium* spp. were able to establish even in those areas where shading, leaf litter depth and cover had increased through plant invasions.

*Crematogaster peringueyi* occurred only in Renosterveld site 1 (Fig. 10). Even though Renosterveld site 2 (Fig. 11) had exactly the same vegetation type suited to nest building as that of Renosterveld site 1, *C. peringueyi* was not found here. It is suggested that intensive spraying of insecticides for mealybug control in vineyards close by was a possible reason for the absence of arboreal ants in Renosterveld site 2 (Addison & Samways, 2000).

#### 4.2 EFFECTS OF *Linepithema humile* ON LOCAL ANT FAUNA

A major effect of plant invasions is that these go hand in hand with human presence and interference of the landscape. The Argentine ant has invaded Vergelegen and formed a significant component of the ant species assemblage in most of the areas sampled. The results showing seasonal effects using CCA shows that Argentine ant significantly affects

the distribution and changes the entire ant assemblages during certain months. Other studies have also shown that where the Argentine ant dominates, there is a considerably lower ant species diversity and richness (de Kock *et al.*, 1992; Carpintero *et al.*, 2004; Luruli, 2006), and is associated with reduced population of many native and non-native arthropod species, including important predator species and major pollinators of native plants (Cole *et al.*, 1992). Gómez and Oliveros (2003) in a study on Hawaii found that the Argentine ant displaced native ant species that disperse seeds.

Personal observations during this study confirm that the Argentine ant forages actively in Protea flowers, and can be so numerous while doing so, that other ant species are not given the opportunity to forage on the same inflorescence. Results also show that Argentine ants outcompete other ant species, especially some *Camponotus* spp, especially *C. maculatus*-group, *C. mystaceus*-group and *C. niveosetosis*.

In contrast, the Argentine ant correlated positively with *Camponotus vestitus*-group, *Ocymyrmex barbiger*, *Ocymyrmex* sp. 2, *Plagiolepis* sp. 3 and *Tetramorium quadrispinosum*, meaning that they were more abundant in the presence of the Argentine ant. These co-existing species may benefit from ant-induced declines in populations of potential predators. These species may be able to persist for a long period following an invasion of the Argentine ant, and can be considered extremely tolerant. Some *Tetramorium* spp. are known for their tolerance not only to Argentine ant invasions, but also for invasions by *Anoplolepis custodiens* (Samways, 1999).

Other scenarios for the persistence of local species in response to Argentine ant invasions need to be considered: “Ant species in invaded areas are typically generalist, opportunists and open habitat specialists. Many of these species are considered dominant in that they are characterized by large nests, aggressive behaviour, and mass recruitment in response to attack” (Carpintero *et al.*, 2004). *T. quadrispinosum* has the ability to co-exist with the Argentine ant because it is an opportunist (Hoffmann & Anderson, 2003) and also closes its nest entrances to protect itself from invasion (Witt & Giliomee, 1999).

Overall *Camponotus* spp. and *Pheidole capensis* are the most sensitive ants to invasions, by both plants and animal. CCA for pitfall data showed that the Argentine ant rarely co-occurred with *Camponotus* spp. and *P. capensis*. Luruli (2007) found that *P. capensis* was

only at bait stations unoccupied by the Argentine ant. Luruli's (2007) results are consistent with the results of study, as *P. capensis* were only in pitfall traps (at very high abundances) in the complete absence of the Argentine ant.

Luruli (2007) using her bait trap data found that the Argentine ant and *Camponotus* spp. correlated positively with each other. Yet the study here, in contrast, showed that most *Camponotus* spp. were absent in pitfalls where the Argentine ant was present. Possibly these differences are due to *Camponotus* spp. not so much being affected by direct competition with the Argentine ant, but rather, through indirect competition, most probably through the removal of food resources.

The Argentine ant is far more successful at finding food (seeds and inflorescences) than *Camponotus* spp. and *Crematogaster* spp. (Lach, 2007). Lach (2007) also observed that *Camponotus* spp. feeding on *Leucospermum conocarpodendron* exited the inflorescences at the slightest disturbance from other arthropods, such as the Cape honeybee (*Apis mellifera*), indicating that these ants avoid microhabitats where prior disturbance has taken place. It is therefore through indirect competition for food that the Argentine ant succeeds at displacing native ants. It may be possible that *Camponotus* spp. in the CFR may evacuate nests after the depletion of food resources by the Argentine ant.

Luruli's (2007) results however, make it clear that in direct competition for food resources, *Camponotus* is not intimidated by the Argentine ant, and Roura-Pascual (pers. comm. 2007) has observed aggressiveness and hostility between the two genera in the field. Anderson's (2001) designation of the group as 'Subordinate Camponotini' seems to be a misnomer in Southern African ecosystems.

In contrast, some American *Camponotus* respond strongly to contact with hostile ant species. These include nest evacuation and removal of brood colonies by *C. festinatus* Buckley (Lamon & Topoff, 1981). The same study found that *C. ocreatus* Emery and *C. vicinus* Mayr defended their nests through recruitment of the major caste.

The Argentine ant did not dominate the species assemblages significantly during hot/dry February 2006 (Table 10) and cold/wet September 2006 (Table 16), possibly because it is prone to decline in extremes of temperature and may experience desiccation during the

height of summer (Addison & Samways, 2000) throughout the natural sites where the amount of sunlight striking the soil surface is considerably higher than for invaded areas that form a dense canopy cover during the summer months in the CFR. The Argentine ant could also be inactive during colder weather because it may have reached its lower temperature limit in the field (Markin, 1970). This may explain the ant's lack of dominance throughout the sites over time, as many healthy ecosystems also still exist on the farm, most notably the undisturbed fynbos sites along the Hottentots Holland Mountains (section 2.2.3.1, sites 6 and 7).

Overall, the Formicinae were far more sensitive to change than Myrmicinae, which had more species able to adapt to change because of their lack of specialization and opportunism and also had more species co-occurring with *L. humile*. In terms of synergistic changes due to invasions, and in the future, global climate change, it seems that the Myrmicinae will do far better at adapting to these changes.

#### 4.3 CONCLUSION

It seems that pine plantations do not endanger abundant species, but compromise the rarer, more specialist species in the long run. It is during complete invasions (conditions where indigenous plants cannot grow under the dense alien canopy cover) that conditions exist which are so radically different from the previous undisturbed habitat that only an equally different ant species assemblage can occur in the new modified habitat.

From an applied point of view, these results suggest that at least for fynbos, a more open plantation design will be accompanied by higher indigenous ant abundance and species richness. This may, in theory, bring about greater sustainable management in the area, should silviculture ever be considered again as a viable cash crop option. Furthermore, habitat heterogeneity across the landscape is essential to the preservation of specialist species in such agro-ecosystems.

Despite Vergelegen's sterling work in the control of plant invasions, little or no attention has been given to the control of the Argentine ant. This control is important, because Argentine ant seriously impedes the proper working of the fynbos ecological system,

through seed theft and outcompeting local ant species necessary to the propagation of fynbos plants.

This problem may not have been addressed, firstly because this study is the first review of insect activity on the farm, and the problem is only now coming to light, or, because the control of invasive animals poses its own unique challenges.

If Vergelegen Estate, and other farms want to do restoration work (which is one of the aims of their invasive removal programme), they will have to bear in mind that fynbos will only recover to something of its former uninvaded condition if the spread of the Argentine ant on the Estate is controlled.

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APPENDIX A

Ants sampled, showing abbreviations of species names for CCA ordination diagrams.

Formicidae sub-family	Species name	CCA abbreviation	Total
Cerapachyinae	<i>Cerapachys</i> sp. 3	<i>Cer 3</i>	3
	<i>Cerapachys wroughtoni</i> Forel	<i>Cer wrou</i>	1
Dolichoderinae	<i>Linepithema humile</i> (Mayr)	<i>Lin hum</i>	2851
	<i>Technomyrmex pallipes</i> Wetterer	<i>Tech pal</i>	26
Dorylinae	<i>Dorylis helvolis</i> Linnaeus	<i>Dor hel</i>	3
Formicinae	<i>Camponotus angusticeps</i> Emery	<i>Camp ang</i>	6
	<i>Camponotus irredux</i> Forel	<i>Camp irr</i>	1
	<i>Camponotus maculatus</i> -group	<i>Camp mac</i>	18
	<i>Camponotus mystaceus</i> -group Forel	<i>Camp mys</i>	124
	<i>Camponotus niveosetosis</i> Mayr	<i>Camp niv</i>	15
	<i>Camponotus</i> sp. 1	<i>Camp 1</i>	76
	<i>Camponotus</i> sp. 2	<i>Camp 2</i>	40
	<i>Camponotus</i> sp. 3	<i>Camp 3</i>	1
	<i>Camponotus</i> sp. 4	<i>Camp 4</i>	5
	<i>Camponotus</i> sp. 5	<i>Camp 5</i>	1
	<i>Camponotus vestitus</i> -group	<i>Camp ves</i>	20
	<i>Lepisiota capensis</i> (Mayr)	<i>Lep cap</i>	540
	<i>Plagiolepis</i> sp. 1	<i>Plag 1</i>	10
	<i>Plagiolepis</i> sp. 2	<i>Plag 2</i>	48
	<i>Plagiolepis</i> sp. 3	<i>Plag 3</i>	131
Myrmicinae	<i>Crematogaster peringueyi</i> Emery	<i>Crem per</i>	154
	<i>Meranoplus peringueyi</i> Emery	<i>Mer per</i>	1335
	<i>Messor capensis</i> (Mayr)	<i>Mes cap</i>	72
	<i>Monomorium</i> sp. 15	<i>Mon 15</i>	801
	<i>Monomorium</i> sp. 8	<i>Mon 8</i>	342
	<i>Ocymyrmex barbiger</i> Emery	<i>Ocy bar</i>	999
	<i>Ocymyrmex</i> sp. 2	<i>Ocy 2</i>	159
	<i>Pheidole capensis</i> Mayr	<i>Phei cap</i>	2241
	<i>Pyramica</i> sp. 1	<i>Pyr 1</i>	1
	<i>Solenopsis</i> sp. 1	<i>Sol 1</i>	20
	<i>Solenopsis</i> sp. 2	<i>Sol 2</i>	27
	<i>Solenopsis</i> sp. 3	<i>Sol 3</i>	8
	<i>Tetramorium erectum</i> Emery	<i>Tet er</i>	47
	<i>Tetramorium quadrispinosum</i> Emery	<i>Tet quad</i>	1089
	<i>Tetramorium</i> sp. 1	<i>Tet 1</i>	211
	<i>Tetramorium</i> sp. 2	<i>Tet 2</i>	176
	<i>Tetramorium similum</i> -group	<i>Tet sim</i>	30
<i>Tetramorium</i> sp. 4	<i>Tet 4</i>	12	
<i>Tetramorium frigidum</i> Arnold	<i>Tet fri</i>	301	
<i>Tetramorium</i> sp. 6	<i>Tet 6</i>	19	
Total			11994



