

Interactions between habitat disturbances and complexity: the effect on ant communities

By

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Submitted in partial fulfilment of the requirements of the degree Magister Scientiae (Wildlife Management)

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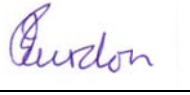
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May 2011

Declaration

I, Jean Purdon declare that the thesis, which I hereby submit for the degree Magister Scientiae (Wildlife Management) at the University of Pretoria is my own work and has not been submitted by me for any other degree at any other tertiary institution.

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Abstract

Hluhluwe-iMfolozi Park is home to a number of indigenous and endemic species. As its mandate is to protect and preserve biodiversity, any factors that may result in the loss of species should be monitored carefully. This study aims to look at two such factors; the alien invasive plant *Chromolaena odorata* and intensive grazing by large mammalian ungulates (resulting in grazing lawns). Disturbances such as these typically result in the modification in

the structural complexity of the habitat which in turn affects its associated fauna. This study compared the structural change of these two disturbances and their adjacent uninvaded habitats and bunch grass habitats respectively. By using a set of manipulated and mensurative (natural) treatments the change in habitat structural complexity was then related to ant diversity, assemblage formation, competitive interactions, resource acquisition, resource monopolisation and ant body size.

Both disturbances revealed that structural complexity within the natural experiments did not significantly alter ant assemblage composition, diversity or competitive interactions. However, at microhabitat scale, as was exhibited by manipulated treatments, structural complexity did appear to play a role in the organisation of ant communities, their competitive interactions and body size. The baited traps which were less complex in structure tended to support the larger species of ants which acquired resources at a faster rate and in higher numbers.

Assemblage composition of ants and the diversity of ants were not significantly altered by *C. odorata*. This could suggest that ants respond to structural complexity rather than plant species richness. Therefore it would be wise to employ the use of other biological indicators such as spiders to test the effect of alien invasive plants on ecosystems. On the other hand, as a result of heavy grazing, a unique assemblage composition of ants was found on grazing lawns when compared with their adjacent bunch grass sites. This would suggest that grazing is a vital component of the savanna system as it adds heterogeneity to the system, resulting in a biodiversity increase.

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“In conclusion,
it appears to me that nothing can be more improving to a young naturalist,
than a journey in distant countries...
the effect ought to be, to teach him good-humoured patience,
freedom from selfishness,
the habit of acting for himself,
and of making the best of every occurrence.”

Charles Darwin, *The Voyage of the Beagle*.

CHAPTER 1

Introduction

Introduction

Globalisation has been shown to be one of the causative agents for the increasing loss of biodiversity (Hansen, 2010). Habitat degradation, overpopulation, modernisation of farming techniques, technological advancements and transport networks are a few of the reasons why species extinction has become common (Vasconcelos, 1998; Steffan-Dewenter, 2010). This creates the need for conservation (Bestelmeyer & Weins, 2001) and the consequent development of appropriate assessment techniques to understand, predict, monitor, and maintain species diversity and composition (Stanton *et al.*, 2002). This has resulted in a number of species or groups of species being used as biological indicators (McGeoch, 1998), which are highly effective in assessing changes in abiotic and biotic factors of the environment (Netshilaphala *et al.*, 2005). In addition, such indicators can be used to monitor the effects of environmental change within a specific area (McGeoch, 1998).

The use of macroinvertebrates as bioindicators is a simple and well-developed procedure that has been used by ecologists in aquatic systems for many years (Metcalf, 1989; Andersen *et al.*, 2004). Dance & Hynes (1980), who worked on two streams, arrived at some interesting results. In the west flowing stream, where the impact of agriculture was intense, the diversity of macroinvertebrate taxa was relatively low. The east flowing stream, although still impacted by agriculture, was not as severely affected as the west flowing stream, and was home to a higher diversity of macroinvertebrate taxa. However, a river of similar size but in pristine condition contained a significantly higher diversity of taxa. A similar result was produced by Delong & Brusven (1998), who analysed macroinvertebrates within a stream that flowed through three distinct geomorphological regions to determine whether the intensive farming practices surrounding the stream had an overall effect on taxa diversity along a longitudinal gradient. Their results revealed that farming in close proximity to the river caused homogenisation of species assemblages along the gradient depicting an unhealthy ecosystem.

The application of such techniques to terrestrial environments has been successfully used in monitoring the rehabilitation of mines in Australia for many years (Andersen, 1997; King *et al.*, 1998). Ants are reliable bioindicators as they act as ecosystem engineers through

processes such as nutrient cycling, soil turning and their interactions with biotic factors (Folgrait, 1998; James, 2004). In addition, ants occupy various niches (generalist predators, scavengers, seed dispersers and competitors) (Andersen, 1995; Sanders & Planter, 2007), are species rich, numerous and easily sampled (James, 2004). They may not reflect the true biodiversity of the area in question but they do show patterns with regards to the loss of diversity of other species (Parr *et al.*, 2002). Therefore, the methodology by which ants are used to monitor mine rehabilitation can be used in other disturbed areas to determine the effects of such disturbances on biodiversity. In this review two types of disturbances will be discussed as well as the consequent effects they have on habitat structural complexity in relation to ant assemblages, ant interactions and the biodiversity of plants and ants.

Disturbances

Disturbances are typically either anthropogenic or natural in nature and occur in both aquatic and terrestrial environments (McNaughton, 1985; Almany, 2004; Archibald *et al.*, 2005). They are known to modify species composition, habitat structure and the biogeochemistry of the ecosystem (Watling & Norse, 1998). In relation to space and time, disturbances can range from the almost insignificant to those affecting very large areas over lengthy periods of time, thereby resulting in a wide variety of responses from the ecosystem (Watling & Norse, 1998). In regards to scale, disturbances may range from very small, such as a bird removing a leaf for the construction of a nest to a catastrophic event such as a tsunami. By looking at these two examples we can clearly see how time and space need also to be taken into account (Watling & Norse, 1998).

The effects of disturbances on the ecosystem depend on a number of factors. The first factor is related to the type and intensity of the disturbance itself (Watling & Norse, 1998; Arnan *et al.*, 2006). For example the effect of deforestation is much longer lasting than a single tree pushed over by an African forest elephant (*Loxodonta cyclotis*) in a forest. Deforestation causes negative long lasting effects on biodiversity, whereas a gap in the canopy layer that has been created by a tree fall can result in increased biodiversity and heterogeneity of the area (Laurance, 1999; Buij *et al.*, 2001). Another factor is that the resilience of an ecosystem is related to its initial state (Watling & Norse, 1998). The continuous modification of grazing lawns in the African savanna by large ungulates has

resulted in a more resilient and stable environment, as they have adapted and responded to change over time (McNaughton, 1985; Archibald *et al.*, 2005). Ecosystems that have not previously been subjected to disturbance, such as pristine fresh-water aquatic systems, may completely collapse and may not recover over time (O'Connor, 1991). Lastly, the effects of disturbance on a particular ecosystem depend on the biotic and the abiotic factors of the environment (Watling & Norse, 1998).

Within an ecosystem, disturbances may affect the environment and its flora and fauna both directly and indirectly (Watling & Norse, 1998). Mobile fishing gear, such as that used for commercial trawling, has a direct effect on the fish it removes from the system and also has an indirect effect on the ocean floor, when the trawl drags on the bottom, thereby modifying the habitat structure (Thrush *et al.*, 1998). This indirectly affects breeding and recruitment of some marine species, especially as many of them are long lived. Modification of habitat structure due to trawling usually results in a less heterogeneous area. For example, it diminishes sites in which certain species are able to hide from predators (Thrush *et al.*, 1998; Watling & Norse, 1998). The same example was true when the effects of grazing on benthic algal population by sea urchins were looked at. Sea urchins directly affected the algal populations by consuming them. However, this resulted in a reduction of algal diversity preventing coexistence between other algal species thereby increasing homogeneity (Paine & Vadas, 1969).

Monitoring of disturbances in all situations is vital to the preservation of biodiversity. This is especially the case in conservation areas which are under pressure worldwide due to the lack of habitat. In South Africa, disturbances within conservation areas are frequent and result in a number of problems (Mgobozi *et al.*, 2008). In order to formulate management plans, the degree, type and effect of the disturbance need to be identified, understood and monitored (Samways *et al.*, 1996). Here I discuss two of the more common types of disturbances in South African game parks, one natural (grazing) and the other anthropogenic (alien invasive plant).

GRAZING LAWNS

During the Late Mesozoic era, fossil records show that the emergence of grass lands and ungulates occurred at the same time. Adaptive radiation of both grasses and wild ungulates

occurred during the Miocene era which was thought to have been due to predator avoidance strategies (Coughenour, 1985; Frank *et al.*, 1998). Gregariousness initiated a substantial amount of pressure on the grasses, resulting in their evolutionary change (McNaughton, 1984). Due to the increased grazing pressure the presence of silica and lignin increased. This occurred on a larger scale in the more arid areas, but the presence of both silica and lignin might possibly have stimulated the evolution of hypsodont dentition of some ungulates (Coughenour, 1985). The digestive tracts, behaviour, cranial and skeletal structure of many of the ungulates are directly related to feeding strategies, all confirming the co-evolution of ungulates and grasses (McNaughton, 1984; Coughenour, 1985; Frank *et al.*, 1998).

In South Africa, the highly diverse savanna biome, which is maintained by an intricate relationship between grass and tree composition (van Langevelde *et al.*, 2003), is severely threatened by human mismanagement and pressures. This has occasioned much attention from conservationists and policymakers, as this biome supports the population of southern Africa both directly and indirectly (Short & du Toit, 2004). Large herbivorous mammals that occupy the savanna ecosystems in Africa generate a substantial amount of pressure on the grassland type communities. These grasses respond to the pressure of herbivory by adjusting their composition and structure, forming grazing lawns (McNaughton, 1985; Archibald *et al.*, 2005).

The formation of grazing lawns does not solely rely on herbivores but also on fire (McNaughton, 1985; Archibald *et al.*, 2005) and high nutrient availability (Cromsigt, 2006). Grazing, however, tends to initiate and maintain the lawns by the consumption of tall bunch grasses (e.g. *Themeda triandra*, *Sporobolus pyramidalis*, *Eragrostis curvula* and *Hyparrhenia filipendula*). Bunch grasses are thought to be less resilient to grazing (Coughenour, 1985) therefore once heavily grazed to a patch they undergo a species compositional shift to stoloniferous lawn grass species (e.g. *Urochloa mosambicensis*, *Digitaria longifolia*, *Panicum coloratum* and *Sporobolus nitens*) (McNaughton, 1985; Archibald *et al.*, 2005; Cromsigt, 2006). These lawn grass species (*Urochloa mosambicensis*, *Digitaria longifolia*, *Panicum coloratum* and *Sporobolus nitens*) show compensatory growth under the influence of grazing, resulting in the maintenance of grazing lawns (McNaughton, 1979; McNaughton, 1985; Painter & Belsky, 1993; Cromsigt, 2006). Grazing also has been shown to increase the quality of the forage in terms of increased nitrogen and protein content. This results in continued grazing by ungulates thereby maintaining the grazing lawn structure

(Adler *et al.*, 2001). Without disturbances such as grazing, an irreversible vegetation species compositional shift may occur. One such example is that of bush encroachment, which occurs in the absence of fire and or grazing (van Langevelde *et al.*, 2003). Another prime example is in the chalk grasslands of the United Kingdom. Unless grazing is maintained, natural scrub returns, which can then revert to woodland. This is undesirable as the grasslands then disappear, reducing biodiversity (Morris, 1967). These two examples clearly indicate the importance of grazing within ecosystems around the world.

Most studies that have focused on the effects of grazing have in the past based their research on the vegetation as a whole (McNaughton, 1979; McNaughton, 1985; Painter & Belsky, 1993; Cromsigt, 2006). In recent times, though, invertebrates as bioindicators have been used in a number of monitoring situations within the grazing lawn ecosystems (Gibson *et al.*, 1992; Seymour & Dean, 1999; Read & Andersen, 2000; Joern, 2005). In response to grazing, invertebrate composition, assemblages and species richness have all been altered. Joern (2005) indicated that grazing influenced grasshopper species richness and species composition. He attributed this to habitat characteristics which were maintained and modified by grazing and its interaction with fire. Gibson *et al.*, (1992), in a similar study, included a number of invertebrate groups. Each group responded differently, which was due to their functional needs. For example, the Coleopteran assemblages remained similar in grazed and ungrazed sites due to their feeding requirements (they are mostly leguminous feeders). Grazing did not affect the most common legumes, therefore providing nourishment and habitat, and preventing number fluctuations. Auchenorrhyncha were found to be affected largely by vegetation height, structure and density, rather than resources. Heteroptera were found to be highly sensitive to grazing due to the modification in habitat structure. This experiment clearly indicates that invertebrate species' reaction to grazing depends on their functional group, their needs and their requirements (Gibson *et al.* 1992). Read & Andersen (2000) used ant functional groups to determine if they could provide an early warning indicator in order to monitor and maintain arid rangelands in Australia. However, the ant functional groups indicated that there was no varying response to differential grazing regimes in the arid region in which the study took place. They concluded that ant species composition in arid regions is largely resilient to disturbances such as grazing.

Studies in Africa using invertebrates as bioindicators are relatively new compared to countries such as Australia. By looking at species richness or diversity one can characterize the various communities, which indicate a healthy environment (Read & Andersen, 2000)

and can be used to determine the effects of invasive plants on species biodiversity (Mgobozi *et al.*, 2008).

BIOLOGICAL INVASIONS

The technological advancements of the nineteenth and twentieth centuries led to improved methods of transport around the world. With this came the movement of various flora and fauna species into areas in which they did not previously exist (Davis, 2003; Cambray, 2004). The introduction of these species in many cases resulted in what is termed biological invasion. This can be described as a process in which a new species arrives in an area where it has never existed before (Crooks, 2002). Often these species become established and have considerable potential to affect the interactions between species at all trophic levels. These biotic invasions are altering the world's biota at an alarming rate for a number of reasons. One reason is the highly competitive nature of these species which often results in a significant impact on indigenous plants because the invasive plants occupy the limited space that is available (French & Major, 2001) and displace native fauna and flora (Gordon, 1998). Secondly, these non-indigenous biota often exhibit prolific breeding and dispersal mechanisms which enable them to inhabit a vacant area more successfully than an indigenous species would. Thirdly, they are in little or no danger from local herbivores and/or pathogens and have the ability to alter the area which they inhabit by changing the disturbance regimes and or resource availability (Gordon, 1998; Crooks, 2002).

Many natural processes are disrupted or changed substantially by the presence of alien invasive species (Zavaleta *et al.*, 2001). These changes may occur at the ecosystem, community or population level. At the ecosystem level invasive species may alter the geomorphological processes (erosion rate, sedimentation rate, elevation and water channels), hydrological cycling (water holding capacity, water table depth and surface flow patterns), biogeochemical cycling (soil or water chemistry, nutrient mineralization and immobilisation rate) and disturbance regimes (type, frequency, intensity and duration) (Gordon, 1998; Crooks, 2002). At the community and population level, effects include: altered stand form (new life form and vertical structure), altered recruitment of natives (allelopathy, microclimate shift and physical barrier), and altered resource competition (light absorption, space pre-emption, water and nutrient uptake) (Gordon, 1998; Crooks, 2002). Along with these disruptions and the interaction with other elements, such as global change, invasive biota are able to inflict large financial costs (management and eradication costs) (Zachariades & Goodall, 2002) as well as damages to managed and natural ecosystems (Zavaleta *et al.*,

2001). This ultimately leads to a substantial loss of biodiversity and change in species composition which is undesirable if a fully functional ecosystem is to be maintained (Zachariades & Goodall, 2002).

One such highly invasive plant that occurs in South Africa is *Chromolaena odorata* L. (L.) King & Robinson (Asteraceae, Eupatorieae). Triffid weed, as *C. odorata* is commonly known, is thought to have first arrived in South Africa in the mid 1940s. It originated from tropical America (de Rouw, 1991) and was then transported to Asia as a winter-flowering ornamental. It was either introduced intentionally as an ornamental (unlikely) or unintentionally (most likely) in packing material that was contaminated with the seed at Durban harbour (Goodall & Erasmus, 1996). *C. odorata* is a perennial shrub that produces bluish-lilac or white flowers at the beginning of the dry season (Goodall & Erasmus, 1996; Zachariades & Goodall, 2002). Production of seeds is prolific and they are transported via wind. The plants exhibit rapid growth (Macdonald, 1983) and form tangled bushes of 1.5-2 m in height. They occasionally reach up to 6 m in height (McFadyen & Skarratt, 1996) with their impenetrable branches shading out indigenous flora and fauna (Macdonald, 1983). *C. odorata* is able to grow in a variety of regions, such as forest, grassland, bushveld (Goodall & Erasmus, 1996) and riverine areas (Macdonald, 1983). *C. odorata* is highly flammable and infests fire sensitive areas. It becomes established on the boundaries of fire sensitive regions and when ignited results in the destruction of some highly diverse systems. This is due to the slow recovery rate of the indigenous species and high fecundity, interference of food production, suppression of desirable species and competitive superiority of *C. odorata* (Macdonald, 1983; Goodall & Erasmus, 1996; Zachariades & Goodall, 2002).

Alien invasive species can affect biodiversity and assemblages of invertebrates in a number of ways; negatively, positively and neutrally (Samways *et al.*, 1996; Gerber *et al.*, 2008). Mgobozi *et al.*, (2008) showed that in South Africa *C. odorata* had a negative effect on spider assemblages, species richness, abundance and diversity. They were all affected in varying degrees, depending on the time *C. odorata* had been present in the ecosystem. Similar results have been produced by Toft *et al.*, (2003) when the effect of water hyacinth (*Eichhornia crassipes*) on invertebrate assemblages was monitored. They discovered that water hyacinth had a greater root system than that of the indigenous pennywort (*Hydrocotyle umbellata*) which had higher leaf coverage. This affected the type of insects associated with the plants. Where water hyacinth prevailed there was a higher abundance of insects that utilise root systems. Fish diets revealed fewer invertebrates associated with the water

hyacinth than those living adjacent to the pennywort. This example provides substantial evidence as to why invertebrates are successful bioindicators.

Other studies on the alien invasive plants and the effect they have on invertebrate species richness and assemblages have revealed no significant differences (e.g. French & Major, 2001). French & Major (2001) looked at the effect of an exotic *Acacia* (*Fabaceae*) on ant assemblages in the fynbos of the Western Cape in South Africa. They showed that there was no significant difference in species richness between invaded and non-invaded areas. However, some slight variations in ant assemblage compositions were noted. This indicates that ant assemblage composition may be better indicators than species richness when looking at the effect of invasive plants on invertebrates. There have also been some recorded instances where biological invasions have facilitated native species (Rodriguez, 2006). A review by Rodriguez (2006) showed that 61 studies provided evidence that exotic plants facilitate indigenous species. He concluded that this was due to the modification of habitat through direct and indirect effects.

By looking at these two examples of disturbances, grazing by large ungulates and invasion by exotic plants, we can clearly see that invertebrate assemblages respond to the changes in the vegetation species richness, composition and structure (Samways *et al.*, 1996; French & Major, 2001; Gerber *et al.*, 2008). Plant species richness has been found to be positively related to invertebrate species richness. An increase in vegetation diversity would consequently lead to higher resource availability for the consumption and use by the invertebrates (Schaffers *et al.*, 2008). Haddad *et al.*, (2001) found that plant species richness had a significant positive effect on insect species richness. The same results have been produced from agricultural monocultures (Armbrecht *et al.*, 2005). In a Colombian coffee plantation, ant species assemblages were compared in areas of pristine forest and in farms with differing management plans. Intensification of agriculture reduced species richness, which confirms that a reduction in plant species richness has a negative effect on invertebrate species richness. Ant species richness also varied with the type of management applied. Farms where no shade was provided the majority of the forest species were absent, concluding that vegetation heterogeneity is important to ant species richness (Armbrecht *et al.*, 2005). Schaffers *et al.*, (2008) used a number of factors (plant composition, structure, flowering diversity as well as some biotic and abiotic environmental variables) to predict insect and spider assemblages. They concluded that the best predictive factor in regards to insect and spider assemblages was plant species composition. This supported their

hypothesis that because plant species composition consists of various other factors it would best describe arthropod assemblages.

Disturbances such as those produced by invasive plants result in the homogenisation of the vegetation (Crooks, 2002); others such as grazing may increase heterogeneity (Seymour & Dean, 1999). Grazing may also decrease heterogeneity due to the over abundance of ungulates and lack of other suitable pastures (Seymour & Dean, 1999). This, as seen above, has a direct influence on invertebrate species richness and assemblages (Schaffers *et al.*, 2008). However, the effect of disturbances on the structural complexity of the habitat also needs to be taken into account. For instance habitat complexity may influence vegetation composition which in turn may initiate responses from invertebrate assemblages, compositions and species richness (Lassau & Hochuli, 2005). In this thesis the term “structural habitat complexity” or “structural complexity” will be used to describe the physical structure of the vegetation. This is not to be confused with diversity or heterogeneity of the vegetation. For example a grazing lawn may be diverse in regards to plant species richness but may be less structurally complex than its adjacent bunch grass habitats. The opposite may be true for invasive plants which typically reduce species diversity but increase in structural complexity.

Structural habitat complexity

Disturbances such as grazing by large ungulates and the occurrence of alien invasive plants may alter habitat complexity either positively (alien invasive plants) or negatively (grazing) (Gibson *et al.*, 1992; Crooks, 2002). Grazing typically alters vegetation architecture resulting in a less complex system. However, alien invasive plants, are often able to modify areas into habitats that are high in complexity (Crooks, 2002). Although areas invaded by alien plants are termed complex, they are generally homogeneous in regards to the vegetation composition. This is due to a number of reasons, but mainly because of their ability to outcompete natural vegetation and because of the lack of natural predators, as described earlier (Crooks, 2002). But, what does this mean in regards to species richness?

Species richness is positively related to habitat diversity in a number of organisms, including birds (Rotenberry & Wiens, 1980; Hurlbert, 2004), insects (Lassau & Hochuli, 2005; Lassau *et al.*, 2005), mammals (Tews *et al.*, 2004), marine organisms (Almany, 2004), fresh water macroinvertebrates (O'Connor, 1991) and ants (Pik *et al.*, 2001). This has been attributed to structurally diverse habitats providing more available niches and resources

which organisms are able to exploit readily (Lassau & Hochuli, 2005; Lassau *et al.*, 2005). An example of this occurred in a study comparing beetle diversity with habitat diversity (Lassau *et al.*, 2005). Beetles are known to occupy a variety of niches within the food web as they are the largest group of insects. Therefore an increase in habitat complexity would increase the amount of detritus, plants, seeds, fruit, carrion, fungus and other small invertebrates on which a number of beetles from varying functional groups could feed. Lassau *et al.*, (2005) confirmed this theory by producing results that positively related beetle species richness to habitat diversity. This theory was also thought to be the case in regards to ant species richness (Pik, 2001). However, in light of more recent studies, results indicate that this is not the case and species richness decreases with increasing habitat structural complexity (Lassau & Hochuli, 2004; Lassau *et al.*, 2005). As habitat complexity increases the microclimate is altered significantly resulting in unfavourable conditions for ants. Lassau & Hochuli, (2004) and Lassau *et al.*, (2005) attribute these results to a number of reasons. Firstly, architectural change in vegetation provides more shelter, shade and a higher leaf litter content resulting in lower temperatures, and higher soil moisture content. Secondly, the majority of ants are highly thermophilic requiring higher temperatures for maximum efficiency. Reduced habitat complexity allows higher radiation on to the ground surface benefiting the majority of ant species. Thirdly, active foraging and the following of chemical cues may be inhibited due to complex vegetation structure. The family Formicidae may be one of the few exceptions when it comes to their responses to habitat complexity – instead of a more complex habitat leading to increased species richness, as would be expected, ant species richness often decreases as a habitat becomes more complex (Lassau *et al.*, 2005).

Invasive species do not increase plant diversity but do increase and alter the structural complexity of the habitat resulting in homogenisation. The effect of habitat complexity on the invasive Asian shore crab (*Hemigrapsus sanguineus*) was studied by Lohrer *et al.*, (2000). The study revealed that as the availability of shelter increased so did the number of Asian shore crabs. An increase in shelter resulted from the modification of the habitat from simple to complex using different size rocks and stones. They concluded that in time the crab will continue to invade the east coast of North America, especially in rocky shores. However, due to the lack of rocky shore along the south-eastern coast invasions of the Asian shore crab may be limited. Homogenous systems such as those produced by alien invasive plants are thought to sustain lower species richness (Mgobozi *et al.*, 2008). Hansen (2000) who studied assemblages of leaf litter microarthropods found that monotypic litter supported a lower oribatid species diversity than more diverse leaf litter.

The intermediate disturbance hypothesis states that both low and high grazing intensities will reduce species diversity. However, grazing at an intermediate level will support a high diversity of species (Wilkinson, 1999). Mgobozi (2007), using ten year old experimental exclosures in Hluhluwe-iMfolozi Park related spider diversity to grazing intensity. Each exclosure consisted of three treatments, naturally grazed, no grazing and intermediate grazing. Her results showed intermediate grazing resulted in the highest diversity of spiders, compared to the other treatments.

Some of the mechanisms that attribute to high species richness in complex habitats are predator prey interactions, competitive interactions and the size of the organisms associated with the vegetation interstices (Sarty *et al.*, 2006). These will be further discussed in detail.

PREDATION

Habitat complexity can affect a number of predator-prey interactions. With an increase in refuge areas and a reduction of predator prey encounters, complex habitats can reduce predation significantly (Almany, 2004; Grabowski, 2004). Goteceitas & Colgan, (1989) looked at the effect of habitat complexity on the foraging success of the largemouth bass (*Micropterus salmoides*) on juvenile bluegill sunfish (*Lepomis macrochirus*) and whether it followed a linear or non-linear pattern. They discovered that an increase in habitat complexity resulted in reduced juvenile bluegill sunfish fatalities. More importantly they found that once a certain threshold of habitat complexity was reached, the effects of predators on their prey were reduced. Juvenile bluegill sunfish chose areas of refuge with a certain density of vegetation, leading to the conclusion that the relationship between predators and habitat complexity is non-linear. Kelaher (2003) provided substantiating evidence for the non-linear relationship between habitat complexity and its effect on predators and their prey. By manipulation of habitat structure using artificial coralline turf with loosely and tightly packed fronds the effect of habitat complexity was determined. The tightly packed fronds negatively affected gastropod species richness, which was thought to be due to a number of reasons. Firstly, an increase in fronds resulted in a decrease in the amount of sediment available (detritus) which is an important food source for the gastropods, thus a reduction of resources. Secondly, the gap sizes were reduced in habitats with a higher density of fronds. This may have resulted in the gastropods being unable to find refuge from predators as the interstitial spaces may have been too small. He too concluded that there is a non-linear

relationship between habitat complexity and predators and once a certain threshold has been reached species richness starts to decline.

Not all interactions between habitat complexity and predation may be as severe as the examples mentioned above. James & Heck Jr. (1994) discovered that the modification of habitat complexity resulted only in the type of foraging behaviour being changed. When artificial seagrass was present the lined seahorse (*Hippocampus erectus*) used an ambush strategy while foraging for prey. However, when artificial seagrass was absent the seahorse would actively forage for prey. Habitat complexity in this situation had no effect on species richness, whereas it did change the type of foraging behaviour.

When looking at the examples mentioned above one can conclude that the effect of habitat complexity on predator prey interactions may depend on a number of factors (Mattila, 1992; Almany, 2004). For example, are the prey species able to utilise the complex habitat in a beneficial way (Mattila, 1992). What type of foraging behaviour is used, and how does this interact with the prey? What are the indirect effects on species competitive interactions and interspecific competition? More studies on these aspects would provide valuable information in order to manage and conserve biodiversity by providing predictive analytical tools in regards to human mismanagements and habitat homogenisation (Almany, 2004).

COMPETITIVE INTERACTIONS: THE DISCOVERY VERSUS DOMINANCE THEORY
Interspecific competition which is thought to enable coexistence plays a vital role in structuring and shaping ant communities (Fellers, 1987; Human & Gordon, 1996; Leburn & Feener, 2007). In order for ants to occur in similar niches there is a need for trade-offs between species (Salvolainen & Vepsäläinen, 1988). Trade-offs may occur in a number of ways. For example some ant species are able to tolerate higher temperatures than others. This allows foraging at different times of the day and in areas of varying complexity (Salvolainen & Vepsäläinen, 1988).

Another such trade-off is the discovery dominance trade-off (Fellers, 1987). When accessing resources ants display one of two types of competition, either interference competition or exploitative competition (Adler *et al.*, 2007; Lebrun & Feener, 2007). Interference competition occurs when ants compete with each other, either as a colony or individually in order to dominate the resource. Exploitative competition relies on the ability of the scouts to locate resources faster than their rival colonies. Because ants separate their workers into either scouts or recruits, they are able to focus energy on only one type of competition (Sarty *et al.*, 2006). If an ant species practises exploitative competition they

invest the majority of their time and energy in scouts, which generally depend on small food supplies (Davidson, 1998; Holway, 1999). However, species that invest much time and resources on recruitment are known to follow the interference type of competition. They discover new food resources at a slower rate than ants using exploitative competition. Once the resources have been discovered they are able to monopolise them, displacing any other ant species that are in the vicinity. One can therefore conclude that ants which use the exploitative competition strategy are generally subordinates, while those that follow the interference type of competition are dominants, consequently giving rise to the discovery dominance trade-off theory (Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007).

There have been a number of conflicting reports in regards to the discovery dominance trade-off theory. An early study conducted by Fellers (1987) found that two categories of ants were present when baits were set: 1) aggressively dominant species and 2) submissive, subordinate and less aggressive species. The subordinate species were highly skilled in locating resources while the dominants were better prepared in defending their resources and in displacing other ants from the baits. At some of the baits, it was noticed that a very small ant *Leptothorax curvispinosis* coexisted more frequently. This was attributed to its small size, which rendered it too small to remove any substantial amount of food. Consequently it did not pose a threat to any of the other species. Fellers (1987) concluded that there is clearly a trade-off between dominants and ants discovering resources, indicating the presence of competition. A number of studies have shown that invasive ants are able to break the discovery dominance trade-off (Holway, 1999; Human & Gordon, 1999; Lach, 2005; Sarty *et al.*, 2006; Rowles & Dowd, 2007). Sarty *et al.*, (2006) found that the yellow crazy ant, (*Anoplolepis gracilipes*) displaced native species and did not comply with the discovery dominance trade-off theory. They attributed this to their dominant aggressive behaviour and numerical advantage. It was also thought to be a superior exploitative competitor due to a number of morphological attributes. Firstly, Sarty *et al.*, (2006) found that the yellow crazy ant has longer legs, allowing for faster movement over complex vegetation. Secondly, it has the ability to extract a wide range of energy rich resources and, thirdly, it has the ability to hold and transport larger quantities of food than other ants. All this makes the yellow crazy ant far more competitively dominant than most other species of ants, resulting in the breakdown of the discovery dominance trade-off.

Palmer (2003) found that habitat heterogeneity contributes to species coexistence. He looked at the effect of termite induced heterogeneity on the effects of competition and coexistence within an acacia ant guild. The *Odontotermes* termite mounds increase shoot

production of the acacia trees which consequently increase invertebrate prey of acacia guild ants. This resulted in the increased colony sizes of three *Crematogaster* species, more so in the two competitively dominant species, *Crematogaster sjostedi* and *Crematogaster mimosae*. These two species were able to exploit and dominate food resources efficiently. The subordinate species *Crematogaster nigriceps* was not as effective in exploitative competition or interference competition as the dominant species of ants (*C. sjostedi* and *C. mimosae*), contradicting the dominance discovery trade-off theory. However, this example does promote the theory that increased habitat heterogeneity does support higher species richness more effectively than homogeneous habitats and allows for species coexistence (Palmer *et al.*, 2003; Sarty *et al.*, 2007). As shown above, habitat complexity does increase coexistence by disrupting competitive interactions; another way it promotes coexistence is by allowing varying size classes of animals to coexist (Kaspari & Weiser, 1999).

SIZE-GRAIN HYPOTHESIS

The size of an organism shapes the way in which it interacts with and regards its own environment (Espadaler & Gomez, 2001). Kaspari & Weiser (1999) coined the term “the size-grain hypothesis” (SGH), which describes how size plays an important role in species distributions, patterns and assemblages. Since then a number of studies have been conducted to try and confirm this theory (e.g. Parr *et al.*, 2003; Sarty *et al.*, 2006). What the SGH suggests is that the smaller the organism the more complex it perceives the environment. However, as the size of an organism increases so does the length of its legs thereby decreasing the energy cost of movement. Organisms with longer legs are able to move faster and more efficiently over vegetation, especially in areas that are low in habitat complexity. However, when a habitat becomes complex in nature the benefit of long legs may become too costly as the organism may not be able to reach resources through small interstices. In complex environments it has been suggested that it would be more efficient for organisms to retain small legs in order to move through the interstices and gain access to resources (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006).

The SGH has been tested in conjunction with habitat complexity, and is thought to mediate coexistence (Sarty *et al.*, 2007). Due to the varying degrees in interstitial sizes of the vegetation, different species may occur in a similar habitat. Sarty *et al.*, (2007), in an experiment conducted on Tokelau, found that smaller ant species were able to access resources within small interstices. The larger usually dominant invasive yellow crazy ant was unable to access and dominate baits in structurally complex environments whereas in simply

structured environments it dominated food baits, thereby supporting the theory that complex habitats promote coexistence. Parr *et al.*, (2003) tested the theory of the SGH in an African savanna between burnt (simple environment) and un-burnt (complex environment) plots. They found no evidence to support the SGH as small ants were more abundant in the planar environment and very few species specific ants occurred in the complex habitat. Fraji-brener (2004) attributed their findings to the evolutionary history of the ants occurring in that area. As patch burning usually occurs ants may not have been able to evolve to fit the SGH. He also concluded that as ants are able to fly over great distances the SGH may not apply due to inconsistencies between ants and their environment. They both concluded that more work needs to be conducted on the SGH in order iron out the discrepancies.

In conclusion, although much work has been done on habitat complexity and disturbances, the work poses many more questions and uncertainties. This thesis attempts to answer a number of pending questions relating to these two types of disturbances.

Thesis structure

This study was conducted in Hluhluwe-iMfolozi Park (HIP) which is situated in the north of KwaZulu-Natal between the latitudes 28°00' and 28°26' and longitudes 31°43' and 32°09' in South Africa (Macdonald, 1983). The park consists of a northern section (Hluhluwe, 225 km²), a southern section (iMfolozi, 447 km²) and the corridor (227 km²), a total of approximately 900 km². Altitude varies from 60-750 m above sea level, owing to the hilly terrain of valleys and ranges. The wet season occurs between the months of October and March. Hluhluwe receives a greater mean annual rainfall of 985 mm; the iMfolozi section a mean of 650 mm per year. The average daily temperatures range from 13°C to 35°C (Cromsigt, 2006). The physiognomy of the park may be described as including forest, woodland, open woodland, thicket, induced thicket and grassland. The vegetation and the environment are described in detail by Whateley & Porter (1983).

I investigated the effects of two disturbances on the structural habitat complexity. The first disturbance was that of the invasive alien plant *C. odorata*. The second disturbance was the grazing by large ungulates. After determining if structural habitat complexity was significantly altered by either or both of these disturbances it was subsequently related to ants. It is hypothesised that *C. odorata* will increase habitat complexity while grazing will decrease it. Therefore the questions related to the ants will be asked according to these

assumptions. To determine the effect of habitat structural complexity on ants a number of factors are looked at:

1. Is species richness affected by structural habitat complexity and is it correlated to plant species richness?
2. Are ant assemblages significantly different between structurally complex and simple habitats?
3. Does structural habitat complexity influence the ants' abilities to access resources?
4. Does structural habitat complexity influence the sizes of ant present?
5. Does the discovery dominance trade-off exist in either or both structurally simple and complex habitats?

In HIP, the maintenance and preservation of biodiversity is one of the parks' main priorities. By analysing the results of this thesis we hope to ascertain the effects of such disturbances on biodiversity, species interactions and assemblages. The results would help the park to formulate sound management techniques and plans in which biodiversity is concerned.

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CHAPTER 2

How does a structurally complex habitat invaded by *Chromolaena odorata* affect local ant assemblage composition and patterns?

Abstract

In Hluhluwe-iMfolozi Park the alien invasive plant *Chromolaena odorata* (triffid weed) is a major source of biodiversity loss. It results in impenetrable stands where the structural complexity of the habitat is thought to be significantly modified. This study aimed to determine the difference in structural complexity between habitats invaded by *C. odorata* and adjacent un-invaded areas. By using a mixture of natural and manipulated treatments ant diversity, assemblage formation, resource acquisition rate, resource monopolisation, competitive interactions and ant body size were related to habitat structural complexity. The data show that *C. odorata* did not affect the diversity or assemblages of the ants, although structural complexity was significantly altered. The natural treatments revealed that only ant body size was affected by *C. odorata*. At a micro habitat scale, however, the manipulated treatments indicated that ants were faster, larger and higher in numbers at the more simple treatments. This study indicates that at micro-habitat scale structural habitat complexity does play a significant role in the formation and organization of ant communities.

Introduction

South Africa is a highly diverse country that is home to a number of endemic flora (Helme & Trinder-Smith, 2006) and fauna species (Gelderblom & Bronner, 1995). Many of these species are currently under threat due to the impact of globalization (Aggarwal, 2006) or have become established where they did not previously exist (Davis, 2003; Cambray, 2004). This has resulted in a number of undesirable biological invasions ranging from diseases such as Rinderpest (Crooks, 2002) to the introduction of *Chromolaena odorata* (triffid weed) (L.) King & Robinson, a highly competitive plant (Goodall & Erasmus, 1995). *C. odorata* was thought to have first arrived in South Africa unintentionally in the mid 1940s (Goodall & Erasmus, 1995) and it is now currently listed as the second most problematic plant in the country (Robertson *et al.*, 2003), after *Lantana camara*. The weed is restricted to frost free areas but, because of global warming, the range of *C. odorata* infestation may increase, resulting in even higher losses in biodiversity (Zachariades & Goodall, 2002). This has created the need for accurate and scientifically proven techniques in order to preserve biodiversity.

Alien invasive plants are known to increase structural complexity of the habitat due to the lack of natural predators (Crooks, 2002). This is because of their abilities to outcompete and smother indigenous vegetation (French & Major, 2001); alter disturbance regimes, ecosystem functioning and process (Gordon, 1998; Crooks, 2002); and finally penetrate ecotones (Zachariades & Goodall, 2002). Habitat structural complexity has been shown in a number of studies to influence the behaviour and diversity of its inhabitants (Nakamura, 2008; Gibb & Parr, 2010). These occur through the modification of competitive interactions (Lassau & Hochuli, 2005; Lassau *et al.*, 2005) or predatory (Almany, 2004; Grabowski, 2004) and foraging behaviour (Goteceitas & Colgan, 1989; Kelaher, 2003) to counteract the structural change of the vegetation. As the complexity of a habitat decreases, so too does the size of the interstices within the vegetation. This enables a wider variety of organisms to inhabit the area as their body size becomes less of a restriction (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006). An environment is consequently created whereby interactions between species become more frequent, thus increasing competitive interactions (Gibb & Parr, 2010).

This study proposes to determine the effect of areas invaded by *C. odorata* on habitat structure and relate it to the composition of ant assemblages and the ability of ants to locate and retrieve resources. Macroinvertebrates, especially ants, have been used in monitoring of

disturbances and rehabilitation for a number of years (Dance & Hynes, 1980; Metcalfe, 1989; Delong & Brusven, 1998; Andersen *et al.*, 2004). This is because of their positive relationship with plant species richness, composition and structure; their numerous roles in regards to ecosystem processes and functioning (Folgrait, 1998; James, 2004); and finally their short life histories (Andersen, 1995; Andersen, 1997). In South Africa the use of such techniques is relatively new and the impact of alien invasive species on indigenous fauna has received little attention. However, Mgobozi *et al.*, (2008) showed that spider diversity and richness were significantly reduced by the presence of *C. odorata*, and species assemblages were different between invaded and non-invaded areas. Another study conducted by French & Major (2001) found that the exotic *Acacia* (Fabaceae) did not reduce ant species diversity, but altered species assemblage patterns.

This study specifically aims to test the effect of habitat structure on resource acquisition, resource dominance and ant body size. The theory on body size was first presented by Kaspari & Weiser (1999) in which they suggested that due to vegetation interstice sizes certain ants would be restricted. This leads to the hypothesis that, because *C. odorata* increases structural complexity of the habitat, ant body size in the *C. odorata* infested areas should diminish. This in turn would have an effect on the competitive interactions, such as the structurally complex habitats infested by *C. odorata* because, in order for species to co-exist, certain trade-offs are required, such as is described by the discovery-dominance trade-off theory (Fellers, 1987; Davidson, 1998; Holway, 1999; Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007; Gibb & Parr, 2010). Ants will either spend their energy on resource discovery or resource dominance; however, structural complexity has been shown to disrupt this trade-off, supporting a higher diversity of less dominant species (Sarty *et al.*, 2006). Additionally, due to extra energy requirements for travel over and through a structurally complex habitat (Gibb & Parr, 2010) such as that presumably exhibited by *C. odorata*, we hypothesize that resources would be accessed more slowly with a lower monopolisation rate than a more structurally simple habitat. This study will aim to take into account seasonal variation using manipulated and natural experiments.

Methods

STUDY AREA

Hluhluwe-iMfolozi Park (HiP) is located in northern KwaZulu-Natal, between the latitudes 28°00' and 28°26' and longitudes 31°43' and 32°09' (Macdonald, 1983). The park consists of

a northern section (Hluhluwe, 225 km²), a southern section (iMfolozi, 447 km²) and the corridor (227 km²), in total approximately 900 km². Altitude varies from 60-750 m above sea level, due to hilly terrain which is broken up by valleys and ranges. The wet season occurs between the months of October and March. Hluhluwe receives a greater mean annual rainfall of 985 mm; the iMfolozi area a mean of 650 mm per year. The average daily temperatures range from 13°C to 35°C (Cromsigt, 2006). The physiognomy of the park may be described as forest, woodland, open woodland, thicket, induced thicket and grassland. The vegetation and the environment are described in detail by Whateley & Porter (1983).

To test the effect of alien invasive plants on habitat complexity and the subsequent effect this has on ants in regards to their assemblages and competitive interactions, two habitats in the Hluhluwe section of the park were chosen, namely the Infested habitat (invaded by *Chromolaena odorata*) (Figure 2.1a) and the uninvaded habitat (an area devoid of *Chromolaena odorata*) (Figure 2.1b). Six sites were chosen from each habitat, all of which maintained maintaining similar characteristics with regard to the Infested and control vegetation composition and structure. These sites were situated a minimum of 100 meters apart to prevent pseudoreplication.

a)



b)



Figure 2.1. Photographs depicting (a) the *Chromolaena odorata* infested structurally complex habitat and (b) the control structurally simple habitat.

VEGETATION SURVEY

Vegetation structure and complexity were surveyed within the two habitats within all 12 sites so as to obtain a standardised version of simple (control) and complex (infested) sites. Within each site, measurements of certain aspects of the vegetation were recorded by placing a pole set distances along an 80 metre transect. In most cases a continuous transect was not possible so sections of the surveys were carried out, covering a total of 80 m. Every 2 m along the transect the height of grass, forbs, small trees and *C. odorata* were recorded, as well as the presence absence of other habitat components such as bare ground, moss, rocks and dead wood that were in contact with the pole. At 4 m intervals distance to the closest tree was measured, while every 8 m percentage canopy cover and potential shading was determined. Canopy cover was visually estimated by using a cylinder 4.5 cm in diameter and 10 cm in height with the observers remaining constant to maintain standards (Gibb & Parr, 2010).

Complexity of the vegetation was determined at 8 m intervals along the transect. A pole was held vertically with 5x6 cm laminated cards attached at 3, 15, 30 and 50 cm. Each card was composed of 20 red dots in a 5 x 4 grid with 1 cm spacing. From a distance of 2 m at eye level the number of red dots visible were counted and recorded. The vegetation structural complexity procedures were conducted twice in the year (July and December) to obtain seasonal differences (Gibb & Parr, 2010).

To determine vegetation composition a quadrat covering 200 m² was placed in each site. Within each quadrat all plant specimens were identified in the field or collected and preserved for later identification in the lab or by an expert. Percentage cover of each species was then classified according to the Braun-Blanquet scale of cover. Environmental aspects, such as rock content, aspect, angle of slope and any other factors that may have contributed to the sites' characteristics were also noted down.

MANIPULATED TREATMENTS

To test the effect of habitat complexity on resource acquisition by ants, ant assemblages and competitive interactions between species of ants, six replicates of four treatments each (arena), were set up in the 6 simple (uninvaded) and 6 complex sites (infested). These manipulated treatments were similar to those used by Sarty *et al.*, (2006) and Gibb & Parr (2010). The four treatments of each arena were designed to be indicative of varying degrees of habitat complexity.

Each arena consisted of a simple card with bait exposed (planar environment); a control (empty microhabitat habitat chamber); a simple microhabitat (large pieces of vegetation from the study site within the microhabitat chamber); and a complex microhabitat (small pieces of vegetation from the study site within the microhabitat chamber) (Sarty *et al.*, 2006). The simple, complex and control treatments were constructed using transparent plastic containers (12.5 cm in height; 14.7 cm in diameter) all containing central observation chambers (5 cm in diameter). The bait card for the planar environment was the same diameter as the observation chamber in the other three treatments. Within each observation chamber and the bait card a fish based protein and honey based carbohydrate was used to attract a variety of species. The honey was placed in a small vial lid (2.5 cm in diameter) while the protein was cut into blocks (1 cm x 1.5 cm) to allow for standardisation and prevent spillage out into the microhabitat chambers. To allow ants access to the baits a series of holes 1 cm in diameter and 1 cm apart were cut into the bottom of observation chambers and the microhabitat chambers.

To prevent ants walking along the bottom of the smooth plastic containers a layer of cotton wool was placed on the bottom. The same was applied to the top of the container, after which a lid was applied to prevent ants entering or leaving without going through the supplied vegetation first. The observation chamber remained open with an easily removable transparent lid (Petri-dish) to open and close, again to prevent ants entering without first going through the microhabitat, thereby maintaining standardisation.

To ensure that simple and complex microhabitats were standardised within each arena a transparency was used to mark out the gaps in the vegetation. The average gap size was determined and used to demarcate simple and complex vegetation structures. The gap size was measured by placing the container holding the experimental microhabitat over a light source. A grid, comprised of 16 points, was placed over the container and the gap closest to each dot was selected. The selected gap was then traced to a transparency and measured to the nearest 0.5 mm. Gap sizes were measured to provide some quantification of the size-gap difference between the complex and simple habitats. The infested structurally complex habitat had an average gap size of 0.283 ($\pm$ 1.46 mm) within the fine treatment and 2.151 ($\pm$ 1.414 mm) within the coarse treatment. The more structurally simple control habitat had an average gap size that was larger in both the fine (0.342 $\pm$ 0.135 mm) and coarse (2.7 $\pm$ 1.733 mm) treatments.

The experiments were conducted twice (July 2008 and January 2009) to obtain seasonal variation. Sites and habitats were completed in no specific sequential order so as to

allow for natural disruptions such as the presence of elephant and black rhino. To maintain the maximum number of species at baits the experiments were started at 08h00 and lasted 3 hours. Temperature was subsequently measured at the start of each experiment and every hour after that till the end. This was done to ensure that temperature was accounted for, and if ant activity was cited as abnormal severe heat or severe cold could account for these differences. Each habitat took 6 days to complete, with each site taking 1 day. Six arenas were placed in a randomised 4 m² block design roughly 20 m apart. Once the experiment commenced the time taken for the first ants to arrive at the baits was recorded. The first ants were then removed from the observation chamber by means of a pooter and placed in a vial for later identification and measurement. Six replicates of each species of ant that arrived first to the baits were mounted and then certain morphological features were measured (e.g. head width above and below the eyes, head length, thorax width, hind femur and hind tibia). Some of these measurements were then used to obtain the body size index (Head width x hind femur) which was related to the size-grain hypothesis.

The occupation of baits, which includes species present, abundance and resource use, was recorded at 1 h, 2 h and 3 h after the start of the experiment. Specimens of unknown ants were collected and placed in vials containing 70 % ethanol to be later identified in the lab and verified by a professional. After the full 3 h of the experiment dominant species were recorded. Dominant ant species are those considered to be monopolising the baits and contain at least five or more of the same species. Any behavioural differences or modification by the ants, throughout the 3 h, were also recorded.

PITFALL TRAPS

Within each of the 12 sites pitfall trapping was used to sample ants, as it is an effective technique by which to determine species richness and diversity. Pitfall traps are commonly used as they are less susceptible to human bias compared with other methods such as active collection (James, 2004). Pitfall trapping in regards to sampling ants is considered to be the optimum sampling method according to the pilot study conducted by Parr & Chown (2001). Due to the presence of many large herbivores in HiP, the pit fall traps were prone to extensive damage. Therefore, many replicates needed to be employed to compensate for this disturbance. Twenty pitfall traps were set up in a rectangular grid (40 m x 30 m) with 10 m spacing between traps in each site. In total, 240 traps were placed in the study area. The traps were sunk into the ground so that the lip of the vial was flush with the surface (Seymour & Dean, 1999). Each trap had a diameter of 52 mm and a depth of 120 mm and was filled with

approximately 2 cm of 50/50 water/propylene glycol as a preservative (Parr *et al.*, 2002; Parr *et al.*, 2004) and a drop of detergent to reduce surface tension (Netshilaphala, 2005). This mixture does not provide a biased situation as it neither attracts nor repels the ants (Parr *et al.*, 2004). The vials were left in the ground for 5 days before collection. In the lab, the ants were separated from other invertebrates and stored in labelled vials containing 70% ethanol (Seymour & Dean, 1999). Pitfall traps that could have been disturbed by animals were excluded from the analysis. Ants were sorted to species level, and either named to species or assigned species code numbers. Species identifications were verified by Dr. Kate Parr.

The trapping occurred on a once-off basis in summer when ant activity was at its highest. This study will be a representative in time of the overall situation. Once-off data collection has been subjected to criticisms but it does reflect certain disturbance levels in regards to abundance levels and total species composition (James, 2004), provided the timing is taken into consideration (Sorensen *et al.*, 2002).

DATA ANALYSIS

To statistically analyse the effect of *C. odorata* on vegetation complexity a two-way ANOVA was conducted using habitat and season in the statistical programme SPSS version 15.0. A similar test was carried out in order to quantify the vegetation structure. Vegetation composition was analysed by first entering the data into a programme called TURBOVEG. The data were then subsequently transferred into TWINSpan (a Two-way Indicator Species Analysis) where the relevés were classified into communities. Refinement was done using the Braun-Blanquet techniques and the results were finally represented in a phytosociological table (Kent & Coker, 1995).

Assemblages of ants from the pitfall traps were all analysed using the programme PRIMER version 6. The raw abundance data were square root transformed in all calculations to weight accordingly the extremely rare and the extremely abundant species while preserving the relative abundance information (Gibb & Hochuli, 2002). To determine the similarity between the two habitats non-metric multidimensional scaling was computed using the Bray-Curtis similarity coefficient. nMDS is the preferred ordination technique when computing and displaying the similarity matrix for assemblage data. By looking at the stress values which range between 0-1, one can determine whether the ordination is a reasonable representation of similarity. The closer to 0 the sample is, the stronger the representation. A two-way ANOSIM was conducted with Bray-Curtis similarities to determine if ant assemblages differed between complex and simple habitats, within the two seasons.

When testing the discovery-dominance hypothesis, data from the first ants arriving at resources and data from monopolisers after three hours were pooled together and square root transformed. The data were tested using a two-way ANOSIM, testing the difference between discoverers and dominants within the simple and complex habitats and again between the summer and winter seasons. A SIMPER test was then carried out to determine how much each species contributed to the differences and similarities between the infested and uninvaded habitats (French & Major, 2001; Gibb & Hochuli, 2002). Approximately 10 of the most common species were ranked in order of their discovery and dominance rates and then plotted. The ants were ranked on a scale of 1 – 8, with 1 being the fastest discoverer and/or the most dominant species (Fellers, 1987; Santini, 2007; Nakamura, 2008; Parr & Gibb, 2009).

To determine if habitat complexity, season and treatment had an effect on resource acquisition time, ant size and monopoliser frequency a three factor full ANOVA model was used. If there was a significant difference between treatments a Kruskal-Wallis test was conducted. This was used to determine the order in which the treatments were accessed. Where there was a significant interaction between treatments a Tuckey's HSD *Post-hoc* test was used.

Results

THE EFFECT OF *C. ODORATA* ON HABITAT STRUCTURE

C. odorata significantly increases the structural complexity ($F_{(1,120)}$, $P \leq 0.0001$) of the natural vegetation structure. Vegetation structural complexity within the two habitats changed significantly over the summer and winter seasons ($F_{1, 120}$, $p < 0.0001$) (Table 2.1). The number of visible dots increased steadily from 3 cm to 100 cm. Only at 3 cm are there not significant differences between the two habitats. The major significant difference between the two habitats was the presence of the *C. odorata* in the infested areas ($F_{(1, 20)} = 4.799$, $P = < 0.0001$) (Table 2.1).

CLASSIFICATION OF PLANT COMMUNITIES

165 plant species were identified within the uninvaded and infested sites. The control site exhibited 132 species, 31 more species than the infested site. The classification of the flora revealed that there were three communities present within the infested and uninvaded habitats. Of the three communities only the first one was split into two sub-communities (Table 2.2).

Table 2.1a. The comparison of the mean number of visible dots at a number of different heights; mean height of *C. odorata*, forbs, small woody trees and grass; mean number of points where wood, litter and bare ground was present; the distance to the closest tree and percentage canopy cover in the infested habitat and the uninvaded habitat. Significant values are in bold and $\pm$ indicates standard deviation. N=12.

	<i>Chromolaena odorata</i> (Complex)	Uninvaded (Simple)	F _(1,10)	P - value
<i>Mean number of visible dots</i>				
3 cm	0.45 (± 0.90)	0.57 (± 0.83)	0.12	0.73
15 cm	2.93 (± 3.00)	6.38 (± 4.58)	7.61	0.01
30 cm	6.03 (± 4.09)	12.46 (± 4.64)	19.18	0
50 cm	8.81 (± 4.72)	17.04 (± 1.97)	40.56	0
100 cm	12.21 (± 3.08)	19.22 (1.04)	66.3	0
150 cm	15.69 (± 2.73)	19.49 (0.82)	20.13	0
<i>Mean height (cm)</i>				
<i>C. odorata</i>	0.89 (± 0.24)	0.00 (± 0.01)	213.78	0
Forb	0.00 (± 0.03)	0.17 (± 0.48)	1.08	0.31
Small woody	0.19 (± 0.17)	0.15 (± 0.14)	0.42	0.52
Grass	0.33 (0.17)	1.48 (± 4.26)	0.88	0.36
<i>Mean number of points where each was present</i>				
Wood	1.42 (± 1.17)	3.25 (± 2.73)	5.19	0.03
Litter	19.5 (± 6.17)	13.33 (± 10.84)	2.83	0.11
Bare Ground	11.08 (± 7.51)	6.25 (± 7.85)	2.35	0.14
<i>Distance to closest tree (m)</i>				
	1.24 (± 0.64)	1.62 (± 3.20)	0.16	0.69
% canopy cover	19.24 (± 15.99)	30.63 (± 21.89)	2.39	0.14

Table 2.1b. The comparison of the mean number of visible dots at a number of different heights; mean height of *C. odorata*, forbs, small woody trees and grass; mean number of points where wood, litter and bare ground was present; the distance to the closest tree and percentage canopy cover in the summer and winter seasons. Significant values are in bold and $\pm$ indicates standard deviation. N=12.

	Summer	Winter	F _(1,10)	P - value
<i>Mean number of visible dots</i>				
3 cm	0.53 (± 0.84)	0.48 (± 0.89)	0.02	0.88
15 cm	5.87 (± 5.12)	3.43 (± 2.64)	3.87	0
30 cm	10.14 (± 6.78)	8.34 (± 3.62)	1.5	0.24
50 cm	12.32 (± 7.18)	13.53 (± 3.30)	0.89	0.36
100 cm	15.07 (± 5.06)	16.36 (± 3.30)	2.25	0.15
150 cm	17.39 (± 3.15)	17.79 (± 2.46)	0.22	0.64
<i>Mean height (cm)</i>				
<i>C. odorata</i>	0.51 (± 0.54)	0.39 (± 0.44)	3.96	0.06
Forb	0.04 (± 0.03)	0.16 (± 0.48)	0.72	0.41
Small woody	0.17 (± 0.18)	0.17 (± 0.13)	0.22	0.65
Grass	0.26 (± 0.18)	1.55 (± 4.24)	1.11	0.3
<i>Mean number of points where each was present</i>				
Wood	1.58 (± 1.08)	3.08 (± 2.88)	3.48	0.08
Litter	16.08 (± 10.09)	16.75 (± 8.72)	0.03	0.86
Bare Ground	10.58 (± 8.92)	6.75 (± 6.58)	1.48	0.24
<i>Distance to closest tree (m)</i>				
	1.72 (± 3.19)	1.15 (± 0.63)	0.36	0.56
% canopy cover	31.95 (± 19.07)	17.92 (± 8.28)	3.63	0.71

Table 2.2. A Braun-Blanquet phytosociological table of the plant species occurring within the six structurally complex relevés of the infested habitat and the six structurally simple relevés of the control habitat.

Community Number	1								2	3
	1.1			1.2						
Relevé Number	5	6	7	8	9	11	1	10	4	1 2 3
Species Group A										
<i>Aristida congesta</i>	1									
<i>Diospyros villosa</i>	1									
<i>Tragia species</i>	1									
<i>Euclea crispa</i>	+									
<i>Ochna barbosae</i>	+									
<i>Grewia caffra</i>	+	1								
<i>Diospyros villosa</i>		a								
<i>Sporobolus africanus</i>		a								
<i>Eucalyptus racemosa</i>		a								
<i>Euclea divinorum</i>		3								
<i>Maytenus senegalensis</i>		1								
<i>Pavonia columella</i>		1								
<i>Acacia nilotica</i>		+								
<i>Acacia robusta</i>		+								
<i>Aerva leucura</i>		+								
<i>Scutia myrtina</i>		+								
<i>Stylochiton species</i>		+								
<i>Cyperus obtusiflorus</i>		+	+							
<i>Mariscus macrocarpus</i>		+	+							
<i>Acacia nilotica</i>			1							
<i>Indigofera cryptantha</i>			+							
<i>Juncus effusus</i>			+							
Species Group B										
<i>Galpinia transvaalica</i>				a						
<i>Gerbera species</i>				a						
<i>Berkheya zeyheri</i>				1						
<i>Phyllopodium cephaloph</i>				1						
<i>Lepidium bonariense</i>				+						
<i>Diospyros lycioides</i>					3					
<i>Grewia flava</i>					1					
<i>Rhus leptodictya</i>					1					
<i>Prismatocarp cordifoli</i>						1				
<i>Acacia karroo</i>					a	1				
<i>Acacia robusta</i>					+	1				
<i>Peltophorum africanum</i>						+				
<i>Cassine aethiopica</i>						+				
<i>Solanum seaforthianum</i>						+				
<i>Rhodomyrtus tomentosa</i>						+				
<i>Lippia javanica</i>						+	1			
<i>Euclea racemosa</i>							1			

Table 2.2 continued. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the infested and control habitats.

Community Number	1							2		3	
	1.1			1.2							
Relevé Number	5	6	7	8	9	11	1	10	4	12	3
Species Group C											
<i>Pavonia</i> species	3	1		1	+						
<i>Melhania didyma</i>	3	1					+				
<i>Gnidia calocephala</i>	1	1		+							
<i>Ziziphus mucronata</i>		+	1	1							
<i>Hibiscus</i> species	1			+							
<i>Dichrostachys cinerea</i>			1	a	4						
<i>Ehretia rigida</i>		1			+		1				
<i>Sida</i> species	+	+	+	+							
<i>Maytenus heterophylla</i>	+	+		+							
<i>Berkheya zeyheri</i>	+				+						
<i>Teucrium kraussii</i>		+				+					
<i>Melinis repens</i>	+			1							
<i>Priva cordifolia</i>		+					1				
<i>Scutia myrtina</i>	+			+		+	1				
Species Group D											
<i>Euclea racemosa</i>									1		
<i>Phyllanthus reticulatu</i>									1		
<i>Urochloa mosambicensis</i>									1		
<i>Berkheya zeyheri</i>									+		
<i>Commelina</i> species									+		
<i>Plectroniella armata</i>									+		
<i>Spirostachys africana</i>									+		
<i>Euclea crispa</i>									+		
<i>Ehretia rigida</i>								1	+		
<i>Dalechampia capensis</i>								+	+		
<i>Acacia karroo</i>								a			
<i>Diospyros dichrophylla</i>								1			
<i>Thunbergia dregeana</i>								1			
<i>Thesium acuminatum</i>								+			
Species Group E											
<i>Chromolaena odorata</i>			4	4	5	4	4	4			
<i>Hibiscus calyphyllus</i>				1			1	3			
<i>Hibiscus trionum</i>				1				+			
<i>Maytenus mossambicensis</i>							1	+			
<i>Cordia caffra</i>				+				+	+		
<i>Hippocratea schlechter</i>				+				1			
<i>Rhynchosia totta</i>				+				+			
<i>Thlaspeocarpa capensis</i>						a		+			
<i>Sideroxylon foetidissi</i>	3	+	+	1			1	+	+		
<i>Solanum panduriforme</i>	+	1		1			a		4		
<i>Commelina erecta</i>	+					1	a	a	+		
<i>Hippobromus paucifloru</i>				3		3		a			
<i>Indigofera</i> species	3								+		
<i>Senna x floribunda</i>	1	+						+	+		
<i>Hippobromus pauciflora</i>	+	1							+		

Table 2.2 continued. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the infested and control habitats.

Community Number	1							2		3									
	1.1			1.2															
Relevé Number	5	6	7	8	9	11	1	10	4	1	2	3							
Species Group F																			
<i>Asparagus minutiflorus</i>													1						
<i>Dalechampia capensis</i>													1						
<i>Gerbera piloselloides</i>													1						
<i>Melhania didyma</i>													1						
<i>Ocimum americ v. ameri</i>													1						
<i>Pavonia columella</i>													1						
<i>Scolopia zeyheri</i>													+						
<i>Asparagus ramosissimus</i>													+						
<i>Hibiscus trionum</i>													+						
<i>Chloris gayana</i>														a					
<i>Dovyalis caffra</i>														a					
<i>Galpinia transvaalica</i>														a					
<i>Setaria sphacelata</i>														a					
<i>Justicia flava</i>													3						
<i>Acrotome species</i>													+						
<i>Canthium inerme</i>													+						
<i>Euclea divinorum</i>													+						
<i>Sida alba</i>													+						
<i>Rhoicissus tridentata</i>													+	a					
<i>Acacia robusta</i>													+	+					
<i>Hypoxis acuminata</i>														a					
<i>Senna x floribunda</i>														a					
<i>Asparagus species</i>														1					
<i>Brachylaena species</i>														1					
<i>Cassine peragua</i>														1					
<i>Cyperus albostriatus</i>														1					
<i>Plectroniella armata</i>											1								
<i>Sideroxylon foetidissi</i>											1								
<i>Canthium inerme</i>											+								
<i>Celtis africana</i>											+								
<i>Diospyros rotundifolia</i>		+																	
<i>Ochna serrulata</i>		+																	
<i>Scolopia zeyheri</i>		+																	
Species Group G																			
<i>Maytenus mossambicens</i>										+									
<i>Sida dregei</i>										+	1	a	a	a	3		1		
<i>Stachys natalensis</i>										1	a	a			3		1	1	
<i>Panicum deustum</i>														1	1		a	4	a
<i>Capparis tomentosa</i>										+					+	+			1
<i>Scutia myrtina</i>												+			a			+	1
<i>Dichrostachys cinerea</i>						+	a		+	1	.								
<i>Hypericum aethiopicum</i>						+	+			1	1								

Table 2.2 continued. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the infested and control habitats.

Community Number	1							2		3		
	1.1			1.2								
Relevé Number	5	6	7	8	9	11	1	10	4	1	2	3
Species Group G continued												
<i>Rhus pentheri</i>						A						a
<i>Sideroxylon foetidissi</i>						A						1
<i>Barleria gueinzii</i>				1								1
<i>Diospyros dichrophylla</i>				1								1
<i>Ehretia rigida</i>						1						1
<i>Gardenia cornuta</i>						.	+					+
<i>Grewia caffra</i>						+						+
<i>Acacia karroo</i>							+					+
<i>Berkheya erysithales</i>							+				3	
Species Group H												
<i>Justicia flava</i>	A	a	3	3	1	A	a	a	3	3		a
<i>Panicum maximum</i>	A	1	a	3	4	3	4	4	4	3	4	a
<i>Ocimum americanum v. americanum</i>	3	3	3	3	1	A			4		1	3
<i>Dactyloctenium australe</i>		3	3	a	a	A	3	a	a	1		
<i>Melhania forbesii</i>	+	a		+		1	1	+				1
<i>Euclea racemosa</i>	A			a	1	A		1		+	+	a
<i>Phyllanthus pentandrus</i>		1		1		1	1		1		1	1
<i>Acacia nilotica</i>	1			1					1	+	+	
<i>Rhus pentheri</i>		1	1				+	+			+	
<i>Zanthoxylum capense</i>		+			+	1	+	1	+			+
<i>Schotia brachypetala</i>		+					+	+				1
<i>Eragrostis curvula</i>	3	a	1	1						1		
<i>Euclea divinorum</i>	A		a	a						+		1
<i>Senna x floribunda</i>			a	3	+	A					+	
<i>Plectroniella armata</i>	1	a		1						+		
<i>Dichrostachys cinerea</i>	A	1						1	a			+
<i>Themeda triandra</i>	A			1							3	
<i>Cordia caffra</i>		1			1		1					1
<i>Maytenus senegalensis</i>	1		1		a					+		+
<i>Rhus pentheri</i>	+			a	1					+		
<i>Ziziphus mucronata</i>	+				a					1	+	
<i>Diospyros dichrophylla</i>	1					1				+	+	
<i>Combretum molle</i>	+			+						+	a	
<i>Berchemia zeyheri</i>		+					1				1	a
<i>Evolvulus alsinoides</i>	+								1		+	
<i>Maytenus heterophylla</i>	+							1	1	+	1	1
<i>Polygala rehmannii</i>	+								1		1	
<i>Gerbera piloselloides</i>	A	1									1	
<i>Peltophorum africanum</i>		1	+									+
<i>Spirostachys africana</i>			1							5		1
<i>Capparis tomentosa</i>			+								+	
<i>Diospyros rotundifolia</i>	+										+	

1. Community 1 is situated in Hluhluwe, where average rainfall is 985 mm. Seven relevés make up community 1, of which five are located in the infested habitat and two in the control habitat. Both sub-communities 1.1 and 1.2 are situated in close proximity to each other (with a minimum of 300 m apart), with similar characteristics in regards to biotic and abiotic factors. Some of the diagnostic species of this community are the trees *Ziziphus mucronata*, *Dichrostachys cinerea* and *Ehretia rigida*; the grass *Sporobolus pyramidalis*; and some forbs *Pavonia* species, *Melhania didyma* and *Gnidia calocephala*. These all occur in species group C. The dominant species all occur from species group I and C and include some trees, *Euclea racemosa* and *Euclea divinorum*; grasses, *Panicum maximum* and *Dactyloctenium australe*; and forbs, *Justicia flava* and *Ocimum americanum* (Table 2.2).

1.1. The three relevés (5, 6 and 7) of this sub-community are also referred to as control sites 5 and 6 and infested site 1 respectively. Relevés 5 and 6 occur a few km away from relevé 7 in close proximity to the Hluhluwe River. However, relevé 5 occurs on top of the ridge while 6 and 7 are closer to the river. In all relevés the topography remains very low at 2°. While both relevés 5 and 7 face west, relevé 6 faces south east and 2% of it is composed of fist sized rocks. The diagnostic species of this sub-community all occur within species group A. Some of these species include the trees, *Euclea divinorum*, *Euclea crispa* and *Grewia caffra*; grasses, *Aristida congesta* and *Sporobolus africanus*; and forbs, *Ochna barbosae* and *Parvonias columella*. The dominant species occurring in this sub-community all belong to species group I and C and include the species of tree, *Euclea divinorum*; grasses, *Panicum maximum*, *Dactyloctenium australe* and *Eragrostis curvula*; and forbs, *Justicia flava* and *Ocimum americanum* (Table 2.2).

1.2. All four relevés (8, 9, 11 and 12) occur within the *C. odorata* habitat and are also known as the infested sites 2, 3, 5 and 6. Both relevés 8 and 9 occur in close proximity to the Hluhluwe River, while relevés 11 and 12 are situated further away from the river and the other two relevés. Relevés 9, 11 and 12 are all situated on north facing slopes, while relevé 8 is south-west facing. The diagnostic species of these four relevés all occur within species group B, while the dominant species occur in species groups I, E and C. Some of the diagnostic species include trees, *Galpinia transvaalica*, *Diospyros lycioides*, *Acacia Karoo* and *Acacia Robusta*; and the forb, *Lippia javanica*. The dominant species of this sub-community include the trees, *Euclea racemosa*, *Zanthoxylum capense* and *Rhus pentheri*; the grasses, *Panicum maximum* and *Dactyloctenium australe*; and the forbs *Justicia flava*, *Ocimum americanum*, *Chromolaena odorata* and *Melhania forbesii* (Table 2.2).

2. Community 2 consists of the relevés 10 and 4, belonging to the infested site 4 and uninvaded site 4 respectively. Both relevés are west facing with the maximum slope angle

being 15°. Relevé 4 is composed of fist sized rocks covering 1% of the area. The diagnostic species of this community occur in species group D. Some of the species include the trees *Ehretia rigida*, *Acacia Karoo*, *Urochloa mosambicensis* and *Euclea racemosa*; the grass, *Urochloa mosambicensis*; and the forbs *Commelina* species and *Thunbergia dregeana*. The dominant species of this community include the grass species *Panicum maximum* and *Dactylocteni australe*, and forb species, *C. odorata*, *Solanum panduriforme*, *Sida dregei* and *Justicia flava* (Table 2.1).

3. Community 3 consists of three relevés 1, 2 and 3, all occurring in the uninvaded site (sites 1, 2 and 3). All three have slopes facing between south and south west, with the topography ranging from 10° at relevé 1 to 30° in relevé 2 and finally 4° in relevé 3. The diagnostic species occur in species group G and include the tree species *Acacia robusta*, *Plectroniella armata*, *Dovyalis caffra*, *Galpinia transvaalica* and *Sideroxylon foetidissi*; the grass species *Setaria sphacelata* and *Chloris gayana*; and forb species *Sida alba*, *Asparagus* species and *Melhanian didyma*. The dominant species include the trees *Dichrostachys cinerea*, *Euclea racemosa* and *Berchemia zeyheri*; the grasses *Panicum deustum* and *Panicum maximum*; and forbs *Stachys natalensis*, *Justicia flava* and *Ocimum americanum* (Table 2.2).

SPECIES RICHNESS, DIVERSITY AND ASSEMBLAGES

Within the pitfall traps, 72 species were recorded, 58 in the infested site and 51 in the uninvaded site. The baited traps recorded 54 species with both the control and infested sites with 33 species each. There was no significant difference between species richness and habitat ($P=0.863$) or abundance and habitat ($P=0.596$). Season also appeared not to have much of a difference in regards to species numbers, with summer having 36 species and winter 30 species. Assemblage composition of ants was compared between the two habitats using data from pitfall traps. The difference between the assemblage composition of ants between the uninvaded habitat and the infested habitat were not significant (Global $R = 0.026$; $P = 0.316$) (Figure 2.2). The four top species that contributed to the dissimilarity (63.37%) of the two habitats were *Pheidole* species G (18.74%), *Anoplolepis custodiens* (7.76%), *Monomorium delagoense* (7.42%) and *Tetramorium constanciae* (5.04%).

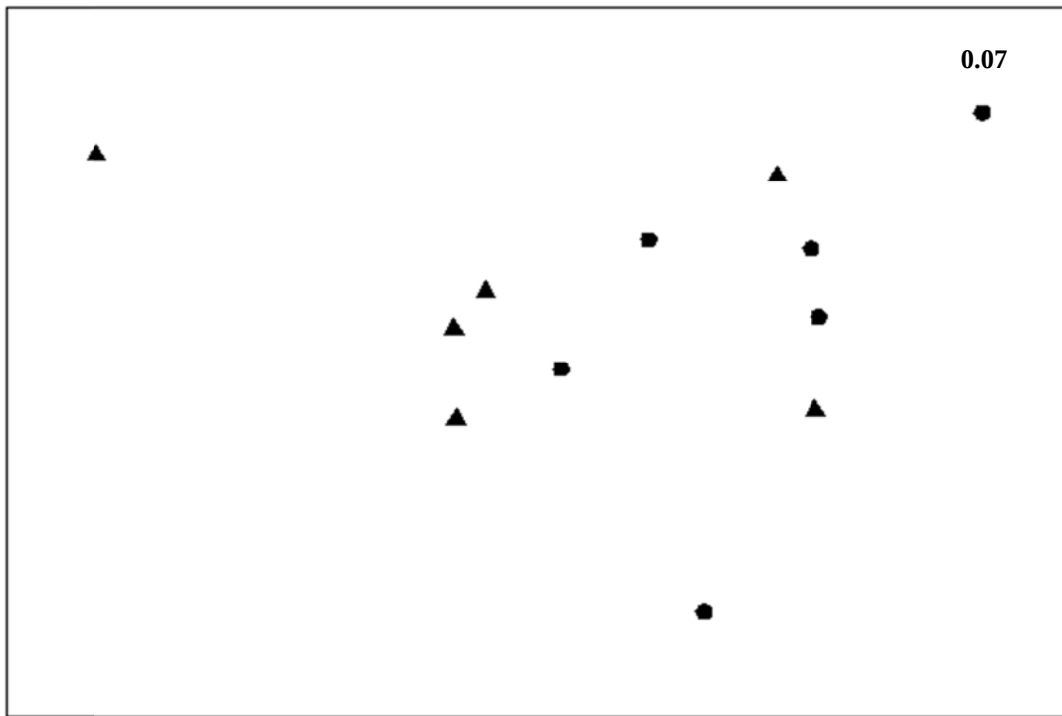


Figure 2.2. A non-metric Multidimensional scaling using Bray-curtis similarities to determine if ant assemblages from the pitfall traps differed between the structurally complex infested habitat and the structurally simple control habitat. R value = 0.026; P value = 0.316.

DISCOVERY AND MONOPOLISATION OF RESOURCES

Discovery rate of resources

The percentage of resources discovered during the summer season was higher in simple habitats at 91.67% (Uninvaded), than in the complex habitats (Infested), with 85.42%. Percentage of occupied resources dropped in the winter season for both the uninvaded and infested habitats to 72.23 % and 68.75 % respectively. When assemblages of ants discovering resources were analysed using a two-way ANOSIM across both seasons and habitats there was a significant difference (Global R = 0.885, $P = 0.001$).

A three factor full model ANOVA was calculated examining the effects of treatment, habitat and season on resource acquisition rate. The results produced were significant in regards to season (ANOVA $F_{(1, 80)} = 41.963$, $P < 0.0001$) and treatments (ANOVA $F_{(3, 80)} = 30.857$, $P < 0.0001$). There was, however, no significant difference between simple and

complex habitats in the natural experiments (ANOVA $F_{(1, 80)} = 30.857$, $P = 0.344$) (Figure 2.3a).

A Kruskal-Wallis test was conducted on the manipulated treatments. Ants arrived at resources fastest at the bait card treatment (28.00 ± 23.15 min), followed by the control (59.35 ± 42.40 min), the coarse treatment (84.13 ± 48.54 min) and finally the fine treatment (117.56 ± 43.22 min). Tukey's *post-hoc* test subsequently revealed that the bait card treatment was significantly different from the control ($P = 0.009$), coarse ($P < 0.0001$) and fine ($P < 0.0001$). Differences between the coarse and control treatments were however insignificant ($P = 0.058$), albeit by a small margin (Figure 2.3b).

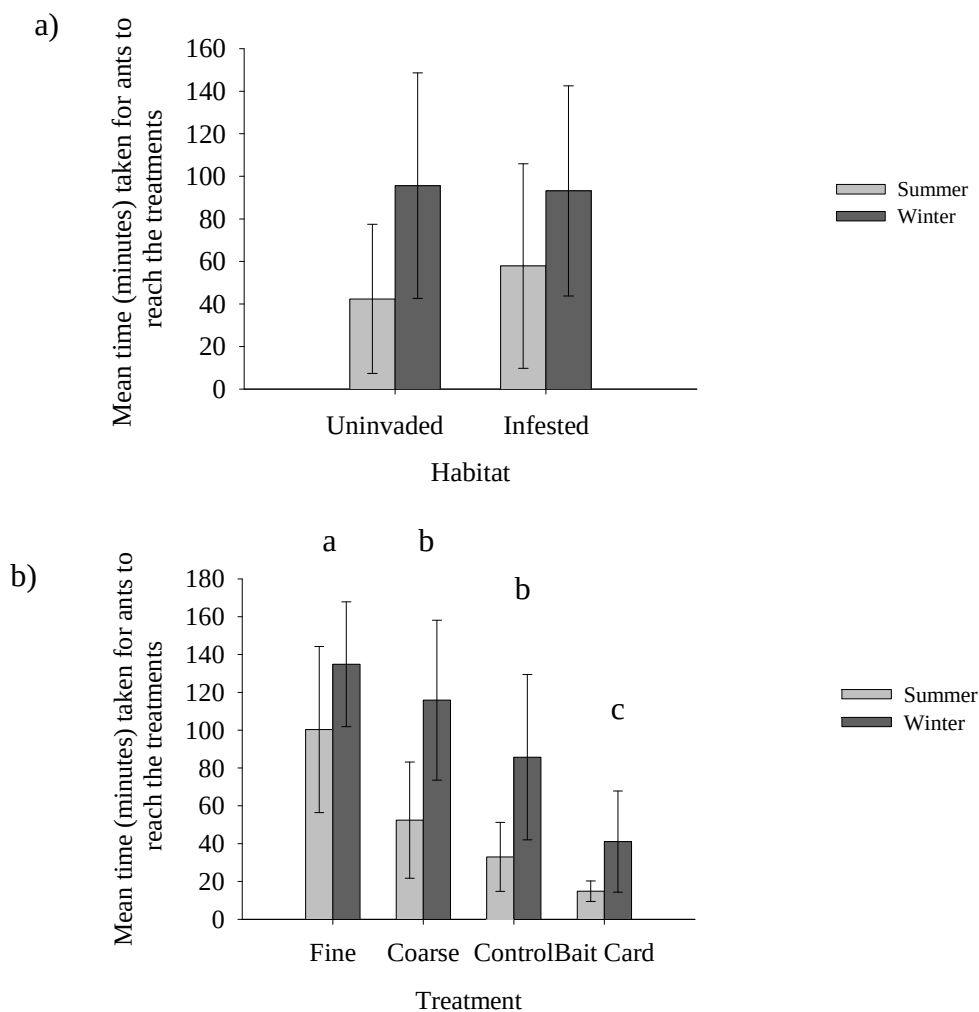


Figure 2.3. Mean ($\pm$) time taken for ants to reach resources when comparing seasons in the a) natural uninhabited and natural infested habitats and b) the manipulated treatments.

Bars with similar letters are insignificantly different.

Monopolisation

The percentage of monopolised baits was expected to be highest during the summer months and gradually increase with time. Although no clear trends were observed, the summer season did have an overall higher percentage of monopolised baits when compared to the winter season. A two-way ANOSIM which looked at the effect of habitat structure across the summer and winter seasons indicated that there was a significant result (Global $R = 0.87$, $P = 0.001$).

The number of monopolised baits followed a similar trend to that of the percentage monopolised baits. There was no significant difference between the natural habitat and the number of monopolised baits (ANOVA $F_{(1, 80)} = 1.651$, $P = 0.202$) (Figure 2.4a). However, between season and frequency (ANOVA $F_{(1, 80)} = 4.396$, $P = 0.039$) and treatments and number of ants (ANOVA $F_{(1, 80)} = 8.214$, $P < 0.0001$) there were significant results. Summer had an overall higher mean number of ants (3.83 ± 1.693) than winter (3.19 ± 1.633). The monopolised resources within the manipulated treatments demonstrated that the bait card had the highest mean number of ants (4.63 ± 1.013). The values then decreased in a systematic order from control (3.79 ± 1.503) to coarse (2.96 ± 1.853) and finally the fine treatment with the lowest frequency (2.67 ± 1.606). Tukey's *post-hoc* test revealed that the fine ($P < 0.0001$) and coarse ($P = 0.001$) treatments were significantly different from the bait card treatment. The control treatment, which revealed similar values to the bait card, fine and coarse treatments, was non-significant (Figure 2.4b).

Discovery versus dominance: Do ant assemblages differ?

A two-way ANOSIM between the discoverers and dominants across the two different habitats revealed a significant differences (Discoverers versus dominants Global $R = 0.053$, $P = 0.184$; Habitat Global $R = 0.606$, $P = 0.001$) (Table 2.3a). When the assemblages of dominant ants were compared to the assemblages of discovering ants in the complex and simple habitats separately there was no significant difference (Infested Global $R = 0.015$, $P = 0.285$; Control Global $R = 0.09$, $P = 0.182$) (Table 2.3b). Percentage contribution of the discoverers was insignificantly different from the percentage contribution of dominant species. Ants discovering the resources and those dominating the resources were mainly composed of four similar species *Pheidole* species A, *Pheidole* species B, *Pheidole* species G and *Monomorium delagoense* (Table 2.3a & 2.3b). When the ants were ranked and plotted on a discovery-dominance plot, there appeared to be no clear correlation between those discovering resources or those dominating them (Figure 2.5).

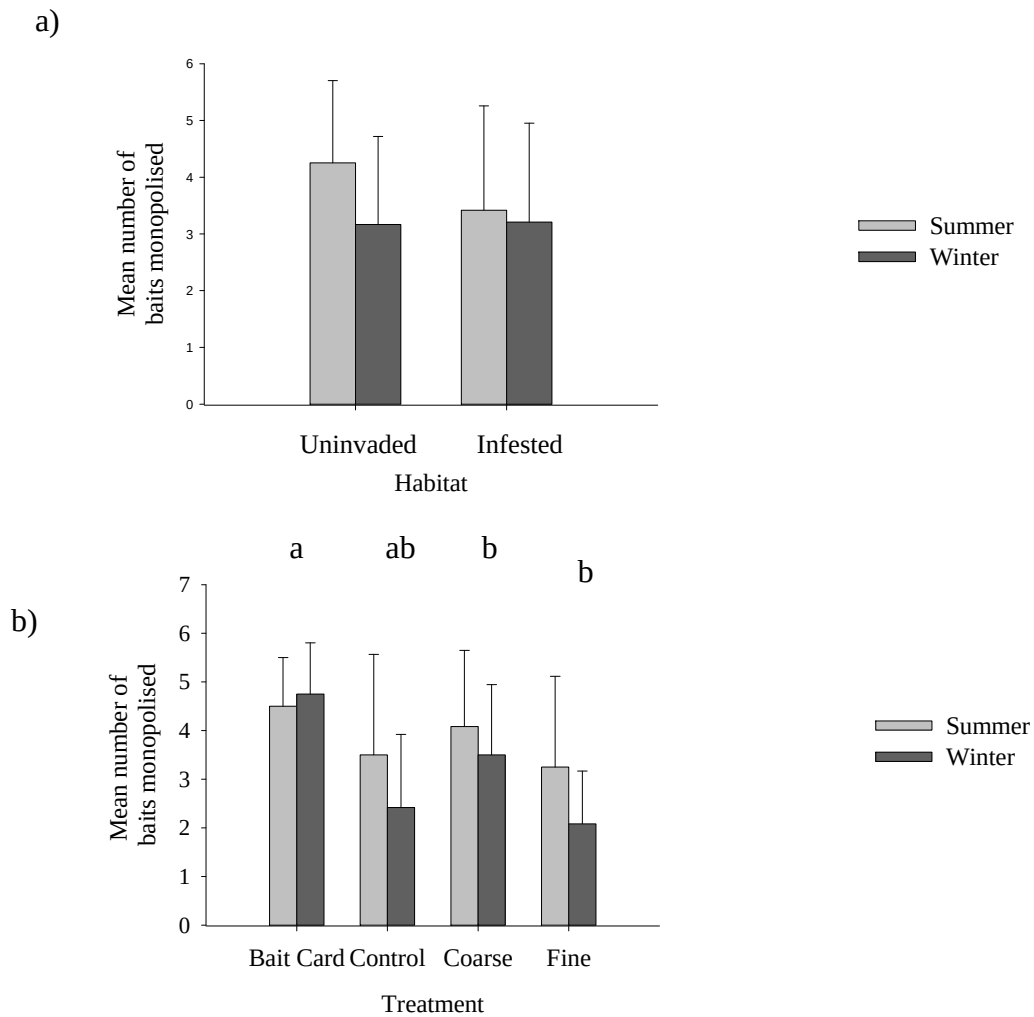


Figure2. 4. Mean ($\pm$) number of baits monopolised by ants during the summer and winter periods when comparing a) the natural structurally complex habitat (infested) and the natural structurally simple habitat (uninvaded) and b) the manipulated bait card, control, coarse and fine treatments. Bars with different letters are significant.

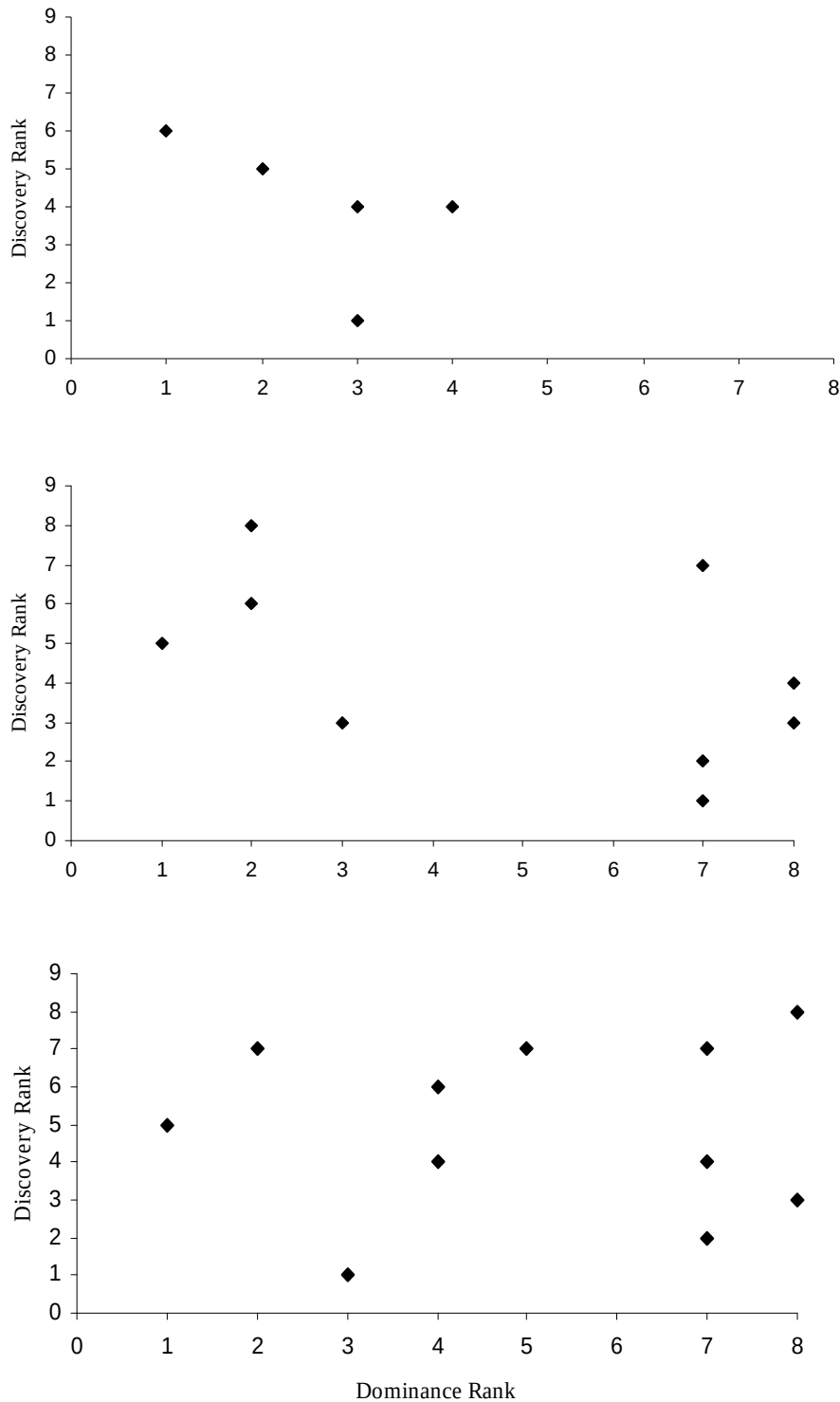


Figure 2.5. A dominance discovery ranked plot of ants in the (a) uninvaded habitat, (b) infested habitat and (c) both habitats combined.

Table 2.3a. A two way SIMPER routine indicating the characteristic species of ants discovering resources and ants dominating resources in the structurally complex infested habitat and the structurally simple uninvaded habitat using data from the baited traps.

Ant species per habitat and season	Average abundance of total	Average similarity of total	% contribution to similarity among level
Discoverers (Average similarity 57.63)			
<i>Pheidole Sp. G</i>	2.46	13.89	24.11
<i>Pheidole Sp. A</i>	1.92	10.97	19.04
<i>Monomorium delagoense</i>	1.54	6.02	10.44
<i>Pheidole Sp. B</i>	1.14	5.67	9.85
<i>Tetramorium Sp. C</i>	1.06	5.36	9.3
<i>Tetramorium Constanciae</i>	1.19	4.43	7.69
<i>Myrmicaria natalensis</i>	0.73	1.75	3.04
<i>Anoplolepis custodiens</i>	0.6	1.41	2.45
<i>Camponotus Sp. A</i>	0.52	1.18	2.05
<i>Monomorium Sp. A</i>	0.35	1.13	1.96
<i>Camponotus cintellus</i>	0.51	1	1.74
Dominants (Average similarity 54.23)			
<i>Pheidole Sp. G</i>	2.12	16.74	30.87
<i>Monomorium delagoense</i>	1.37	8.42	15.53
<i>Pheidole Sp. A</i>	1.25	8.25	15.22
<i>Pheidole Sp. B</i>	0.89	5.93	10.94
<i>Anoplolepis custodiens</i>	0.65	3.07	5.66
<i>Myrmicaria natalensis</i>	0.89	2.67	4.93
<i>Tetramorium Sp. C</i>	0.5	2.67	4.93
<i>Monomorium Sp. A</i>	0.42	1.76	3.25
Uninvaded (Average similarity 51.32)			
<i>Pheidole Sp. G</i>	3.14	23.8	46.38
<i>Pheidole Sp. A</i>	1.13	5.29	10.31
<i>Monomorium delagoense</i>	1.26	4.4	8.58
<i>Pheidole Sp. B</i>	0.7	3.01	5.87
<i>Monomorium Sp. A</i>	0.71	2.89	5.63
<i>Crematogaster Sp. A</i>	0.73	2.22	4.32
<i>Myrmicaria natalensis</i>	0.71	2.2	4.29
<i>Tetramorium Constanciae</i>	0.65	1.78	3.47
<i>Pheidole Sp. H</i>	0.53	1.58	3.08
Infested (Average similarity 60.54)			
<i>Pheidole Sp. A</i>	2.04	13.94	23.02
<i>Monomorium delagoense</i>	1.65	10.03	16.57
<i>Pheidole Sp. B</i>	1.33	8.59	14.2
<i>Tetramorium Sp. C</i>	1.49	8.03	13.27
<i>Pheidole Sp. G</i>	1.44	6.83	11.28
<i>Anoplolepis custodiens</i>	1.12	4.38	7.23
<i>Tetramorium Constanciae</i>	1.11	4.09	6.76

Table 2.3b. Characteristic species of ants from a SIMPER routine discovering resources and dominating resources in (a) the control habitat and (b) the infested habitat using data from baited traps.

a) Uninvaded				(b) Infested			
Ant Species	Average abundance of total	Average similarity of total	% contribution to similarity among level	Ant species	Average abundance of total	Average similarity of total	% contribution to similarity among level
Discoverers (Average similarity 64.88)				Discoverers (Average similarity 69.52)			
<i>Pheidole</i> Sp. G	3.27	19.63	30.26	<i>Pheidole</i> Sp. A	2.25	13.62	19.58
<i>Pheidole</i> Sp. A	1.59	8.7	13.42	<i>Tetramorium</i> Sp. C	1.99	10.98	15.79
<i>Monomorium delagoense</i>	1.42	7.17	11.05	<i>Pheidole</i> Sp. G	1.64	9.09	13.07
<i>Monomorium</i> Sp. A	0.71	5.26	8.1	<i>Monomorium delagoense</i>	1.66	8.36	12.03
<i>Pheidole</i> Sp. B	0.89	4.16	6.41	<i>Pheidole</i> Sp. B	1.38	7.57	10.89
<i>Tetramorium Constanciae</i>	0.93	3.61	5.57	<i>Tetramorium Constanciae</i>	1.45	6.07	8.73
<i>Myrmecaria natalensis</i>	0.73	3.14	4.84	<i>Pheidole</i> Sp. N	0.66	3.58	5.15
<i>Pheidole</i> Sp. H	0.55	2.96	4.56	<i>Myrmecaria natalensis</i>	0.73	3.2	4.61
<i>Camponotus</i> Sp. A	0.91	2.26	3.48	<i>Anoplolepis custodiens</i>	0.95	2.38	3.42
<i>Crematogaster</i> Sp. A	0.66	2.24	3.45				
Dominants (Average similarity 64.98)				Dominants (Average similarity 65.48)			
<i>Pheidole</i> Sp. G	3.01	28.3	43.56	<i>Pheidole</i> Sp. A	1.82	15.1	23.06
<i>Monomorium</i> Sp. A	0.71	8.23	12.67	<i>Monomorium delagoense</i>	1.64	12.71	19.41
<i>Monomorium delagoense</i>	1.1	7.15	11.01	<i>Pheidole</i> Sp. B	1.28	10.52	16.06
<i>Myrmecaria natalensis</i>	0.7	5.31	8.17	<i>Myrmecaria natalensis</i>	1.08	7.17	10.95
<i>Crematogaster</i> Sp. A	0.81	4.47	6.87	<i>Pheidole</i> Sp. G	1.24	6.3	9.62
<i>Pheidole</i> Sp. H	0.5	4.43	6.82	<i>Tetramorium</i> Sp. C	1	5.81	8.87
<i>Pheidole</i> Sp. A	0.68	1.9	2.92	<i>Anoplolepis custodiens</i>	1.29	5.51	8.42

THE EFFECT OF *C. ODORATA* ON BSI (BODY SIZE INDEX)

Both the uninvaded and the infested habitats appear to have a broad spectrum of BSIs (Figure 2.6). The uninvaded site however had a much higher abundance of smaller ants (*Pheidole* G), while the same was true for ants with larger BSI in the infested habitat (*Myrmicaria natalensis* and *Polyrachis shistacea*) (Figure 2.6). A three factor full ANOVA model on the interactions between treatment, habitat and season on the effect of BSI of ants revealed some surprising results. There was a significant difference between habitats (ANOVA $F_{(1, 79)} = 9.786$, $P = 0.002$) with ants having large BSIs' occurring in the *C. odorata* infested areas (Figure 2.6a). A significant interaction was recorded between seasons and the two different habitats (ANOVA $F_{(1, 79)} = 13.436$, $P < 0.0001$), as well as season, habitats and the four treatments (ANOVA $F_{(3, 79)} = 3.115$, $P = 0.031$) on BSI (Figure 2.6). Ants in summer were recorded to have higher mean BSI (1.53 ± 1.37) within the infested areas than those in winter (1.04 ± 0.87). The uninvaded habitat had ants with overall smaller BSI, with winter ants being larger than those occurring in summer (Figure 2.7a).

The manipulated treatments, although significantly different, did not comply with predictions. The Kruskal-Wallis test revealed that the ants with the smallest BSI (0.67 ± 0.354) occurred in the fine treatment. The sizes increased from the coarse (0.90 ± 0.629) to the bait card treatment (1.46 ± 1.16), and then finally to the control (2.09 ± 1.58). Tukey's *post-hoc* test concluded that not all the treatments were significantly different from each other. The fine treatment was similar to the coarse treatment ($P = 0.810$), but significantly different from the bait card ($P = 0.018$) and control treatments ($P < 0.0001$). The coarse treatment was comparable to the bait card ($P = 0.147$), as was the bait card to the control treatment ($P = 0.70$) (Figure 2.7b).

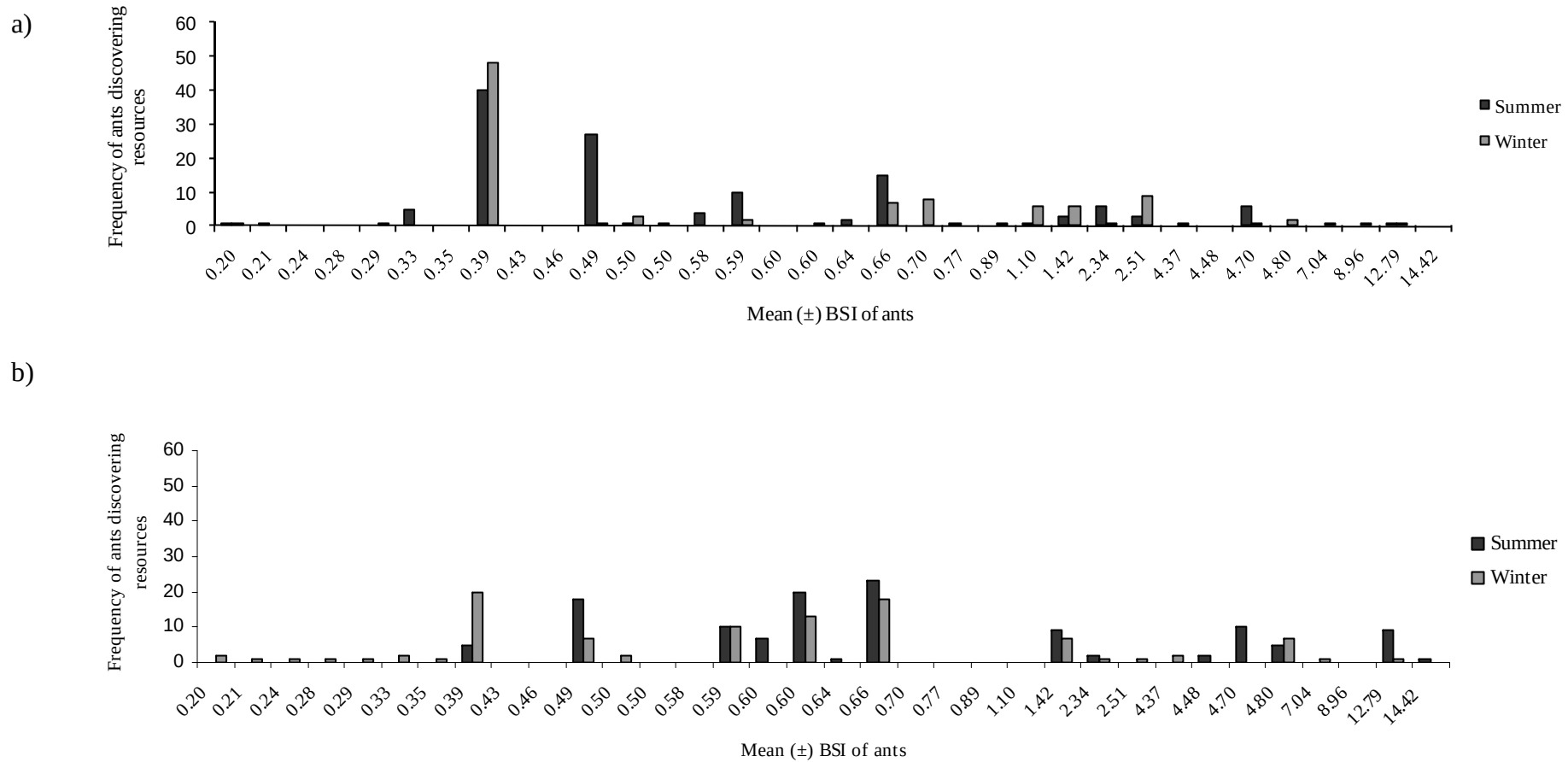


Figure 2.6. Frequency of first ants to arrive at resources within the summer and winter season, comparing the BSI ($\text{BSI cm}^2 = \text{head width} \times \text{total hind leg length}$) between the a) structurally simple uninhabited habitat and the b) structurally complex infested habitat.

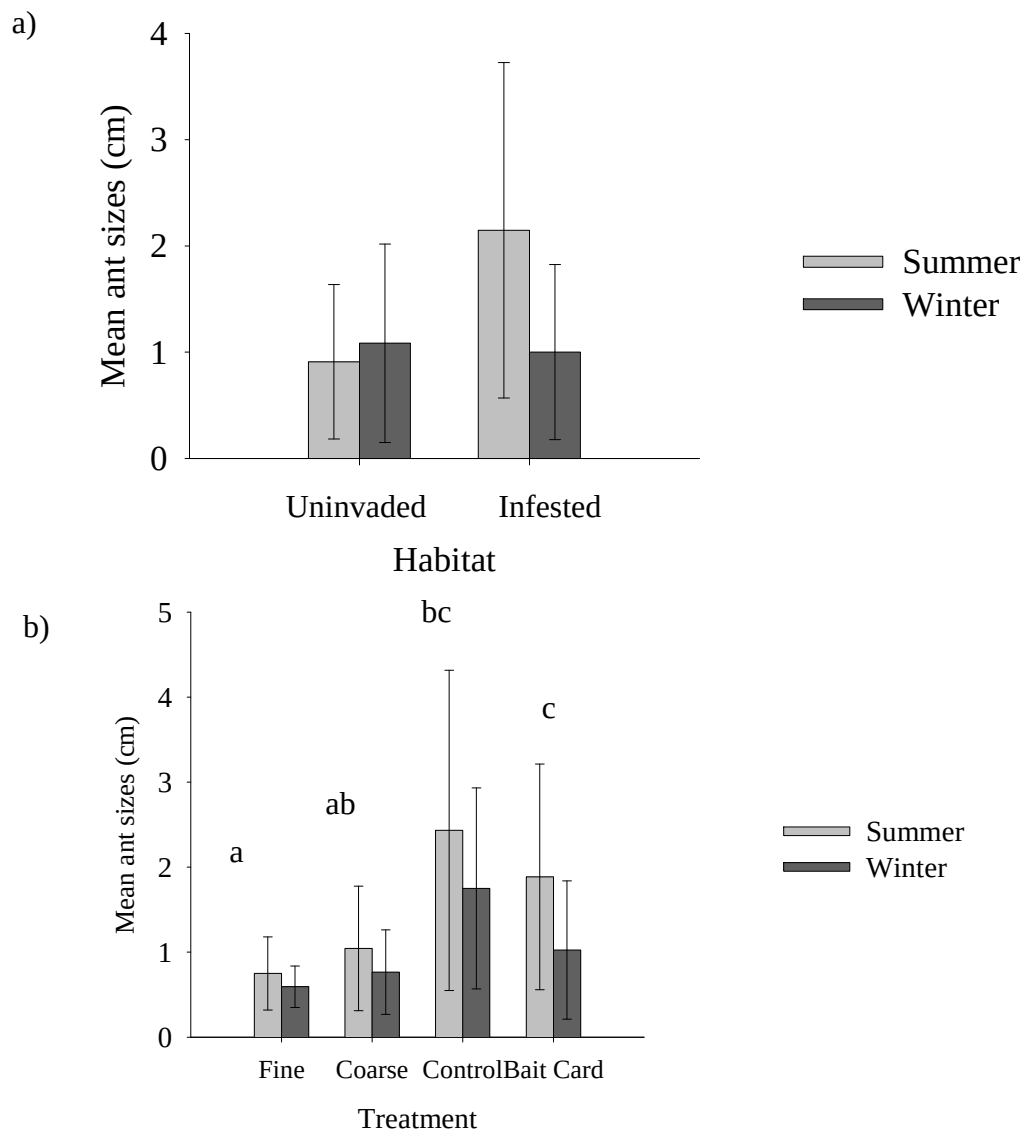


Figure 2.7. Mean ($\pm$) ant BSI (cm^2) for the summer and winter season in the a) natural structurally simple uninvaded habitat and the natural structurally complex infested habitat and b) the manipulated bait card, control, coarse and fine treatments. BSI is the Body Size Index which is calculated by head width x total hind leg length. Bars with similar letters are insignificant.

Discussion

The effect of alien invasive plants on ecosystem functioning and processes is vital to the understanding of the preservation of biodiversity and the formulation of management decisions. This study did reveal that a homogenous, yet structurally complex, habitat invaded by *C. odorata* had significant effects on ant assemblages and patterns in regards to the manipulated treatments. However, the natural habitats did produce some varying and surprising results, suggesting that it is not only habitat complexity that affects ant assemblage composition and patterns, but other factors as well. Such factors include biotic and abiotic influences. This discussion aims to give some insight as to why these particular results may have been obtained.

SPECIES RICHNESS

Within the infested sites, the richness of plant species was significantly reduced when compared with the control sites. This is expected, as alien invasive species are known to reduce native biota (Samways *et al.*, 1996; Gerber *et al.*, 2008, Mgobozi *et al.*, 2008). The reduction of biodiversity by alien invasive plants may occur in a number of ways. Firstly, the alien species may displace indigenous biota by out competing them; secondly they are usually able to breed prolifically, enabling them to occupy niches at a faster rate than native flora; and, finally, they flourish because of a lack of natural predators (Gordon, 1998; French & Major, 2001; Crooks, 2002). Previous studies have indicated that there is a positive relationship between the richness of plant species and the richness of invertebrate species (Haddad *et al.*, 2001; Armbrrecht *et al.*, 2005; Schaffers *et al.*, 2008). However, in this study there appeared to be no difference in ant species richness between the two habitats (Figure 2.2). This could be because ants may not respond to plant species richness, but to plant functional groups instead (Schaffers *et al.*, 2008). Schaffers *et al.*, (2008) conducted a study in the Netherlands to determine which factors - habitat complexity, plant composition (including functional groups, communities and individual species richness) or environmental conditions - best predicted invertebrate species richness. They concluded that plant species composition, using functional groups, produced the most promising results for predicting invertebrate species richness.

ASSEMBLAGES

The delineation of plant communities in this study revealed that there were no distinct differences between the habitats infested by *C. odorata* and those that were not (Table 2.1). This could be another reason as to why there was no difference in species richness or why the pitfall traps indicated no assemblage composition difference between the two habitats (Figure 2.2). The baited traps, on the other hand, did reveal significant differences in assemblage patterns between complex and simple habitats. As the baited traps were designed specifically to test the size-grain hypothesis and discovery dominance trade-off theory, they may not have been adequate for testing overall species assemblage differences. There could be a number of reasons for this, one being that the baited traps were only present for three hours at a specific time of day, which would lead to bias towards certain diurnal ants and those that were restricted because of temperature and predatory constraints (Greenslade & Greenslade, 1971). On the other hand, pitfall traps have been shown in a number of studies to provide the best results for determining species richness and assemblages (Wang *et al.*, 2001). However, the baited traps in this study may have attracted different assemblages of ants owing to competitive interactions and the varying complexity of the habitats. If this is the case, it would result in the acceptance of the discovery dominance trade-off theory (Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007).

The discovery dominance trade-off theory suggests that, in order for species of ants to coexist, they focus their resources into either scouts (exploitative competition) or recruiters (interference competition) (Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007). It also suggests that a simple planar environment is thought to be ideal for higher ant numbers of the more dominant species as it gives them the competitive edge (Fellers, 1987; Lebrun & Feener, 2007). The results of this study revealed no evidence to support the dominance discovery trade-off hypothesis as there was no distinct separation between the assemblages of ants that discovered resources and those that dominated them (Table 2.3a & 2.3b). Nor did the results of this study support the theory that a simpler, less structurally complex environment would provide an ideal habitat for a higher number of ants in the dominant species (Fellers, 1987; Lebrun & Feener, 2007). These results could, however, be attributed to there being no clear delineation between the vegetation communities of the infested and control habitats (Table 2.1). Habitat structural complexity may also have played a major role as, below 3 cm of the vegetation within the uninvaded and infested habitats there was no difference in complexity (Table 2.1). This could be because *C. odorata* is allopathic, leading to diminished ground cover (Goodall & Erasmus, 1996; Zachariades & Goodall, 2002). The

ants that are attracted to the baits are generally surface dwellers that are affected by ground cover. Resources are therefore more readily available in structurally less complex habitats, enabling species access at a faster rate (Gibb & Parr, 2010).

RESOURCE ACQUISITION RATE AND MONOPOLISATION OF BAITS

A complex environment is thought to increase resource acquisition time and well as reduce monopolisation of food sources (Gibb & Parr, 2010). This may be the result of microclimate modification (Lassau *et al.*, 2005, Lassau & Hochuli, 2005). As the habitat becomes more complex, radiation penetration is reduced, while moisture content is increased, thereby reducing temperature. As ants are highly thermophilic (Lassau and Hochuli, 2004; Lassau *et al.*, 2005), a complex habitat could result in decreased activity. It has also been suggested (Lassau & Hochuli, 2004; Lassau *et al.*, 2005) that complex vegetation inhibits the ability of ants to locate and follow chemical cues successfully. This would reduce the number of recruiters at food resources therefore lowering the monopolisation rate (Lassau and Hochuli, 2004; Lassau *et al.*, 2005). As predicted, the complex manipulated treatments were discovered at a slower rate than any of the others (Figure 2.3b) and were monopolised less frequently (Figure 2.4b). As the treatments became less complex the amount of time till discovery of resources was reduced. The monopolisation of baits remained similar in three out of the four experimental treatments. There may be a number of possible explanations for this. One is that the size of the access holes through the microhabitat chambers in three out of the four treatments were all the same. Another more plausible explanation is that monopolisation was determined after 3 hours. By this time, especially in summer, temperatures were high (maximum 40°C minimum 22.7°C), often reducing ant activities. Although ants are thermophilic and prefer higher temperatures, they are also unable to tolerate extremely high temperatures (Kaspari, 1993). This may also explain why, after 3 hours, the monopolisation of resources in both the natural (Figure 2.4a) and manipulated (Figure 2.4b) experiments were only marginally higher in summer than in winter (winter minimum temperature 16.1 °C and maximum temperature 32.6 °C). However, the discovery rate of resources was substantially faster in summer than winter in both natural (Figure 2.3a) and manipulated experiments (Figure 2.3b). Resource discovery generally occurred early on when temperatures remained at what appeared to be an optimal level for ant activity.

In the natural experiments, there appeared to be no difference between simple and complex habitats for either discovery (Figure 2.3a) or monopolisation (Figure 2.4a) of resources. Again, this may be the result of the ground being similar in both complex and

simple habitats (Table 2.1). These results may also be the product of abiotic and biotic factors for which there was no control. This could explain why the manipulated experiments and not the natural experiments complied with predictions. The manipulated experiments were closed environments and were not influenced by normal ecosystem functioning processes. This enabled the varying complexities of the treatments to influence directly the behaviour of the different ant species.

BODY SIZE INDEX (BSI)

The manipulated experiments revealed results that were in accordance with what was expected in terms of the Body Size Index (BSI) (Figure 2.6b). The size grain hypothesis (SGH) predicts that, as the habitat becomes more complex, ant sizes will begin to decrease so as to allow them access through the interstices of the vegetation (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006). In this study, although significant differences were noted, they only occurred between the fine treatment and the control treatment. This may indicate that a certain threshold in habitat complexity is required in order for significant changes in species compositions and, consequently, size to occur. Other studies have confirmed that a particular threshold in habitat complexity is vital in reducing predation affects on prey (Goteceitas & Colgan, 1989; Kelaher, 2003). Habitat complexity is thought to reduce the number of predators as it provides more refuge areas in which the prey can hide (Almany, 2004; Grabowski, 2004). *C. odorata* has also been shown to reduce the diversity of predators such as spiders (Mgobozi *et al.*, 2008), which in turn could have a direct effect on their prey species, which include ants. This could explain the results obtained from the natural habitat experiment (Figure 2.6a), when looking at the size grain hypothesis. The more complex habitat, infested by *C. odorata*, is home to ants with larger BSI than those in the simple control habitat. The predators of the ants may have been displaced by the invasion of *C. odorata*, thus enabling larger ants to take up residence. However, the ants with larger BSI residing in the *C. odorata* may also be the result of the simple planar ground layer. Once again, the threshold of complexity needed to alter significantly the species composition may not have been reached, providing smaller species rather than the larger ones with a competitive advantage (Nakamura, 2008).

Results indicated that the season also played a significant role in the determination of the BSI in both the natural (Figure 2.6a, 2.7) and manipulated (Figure 2.6b) habitats. The summer season was shown to support ants with larger BSI than the winter season (Figure 2.7). One explanation is that larger ants may only forage where and when the smaller ants

are inactive (Kaspari, 1993). This may be a mechanism which allows the various species of ants to coexist. The smaller ants may prefer the cooler temperatures of winter, so displacing the larger ants. In summer, the smaller ants may not be able to tolerate the extreme heat, so allowing the larger species of access to resources. Smaller organisms are known to desiccate much more readily than larger organisms, because of their surface area to body ratio (Kaspari, 1993). This enables species to coexist as a result of seasonal temperatures and the temperatures associated with microhabitat change due to the varying degree of habitat complexities.

Conclusion

Habitat complexity in this study played a significant role in species composition, patterns and assemblages in closed systems, where biotic and abiotic influences are controlled. Within the natural habitats, results were not as expected and varied substantially. As said earlier, this may have been because other factors enabled the ecosystem to function. Secondly, however, these results may have been severely biased by a fire that occurred in three of the control sites three months prior to the pitfall trapping, the Braun-Blanquet survey and summer treatment experimentations. This fire may have been the reason for the absence of differences in plant and ant species richness and the lack of distinction between vegetation communities of the complex and simple habitats. However, the experiments before and after the fire still revealed similar trends within the uninvaded habitat, when compared with those conducted in the infested habitat. One can, therefore, conclude that the fire had no significant effects on the results of the natural and manipulated experiments. Despite the uncertainties, this study does provide some useful insight into how *C. odorata* affects the species of ants, their patterns and assemblages. One could use these results to form management plans when it comes to clearing alien invasive plants and subsequently rehabilitating the veld. However, in order to obtain the full picture in regards to the effect *C. odorata* has on its associated fauna, much more research needs to be undertaken on the biotic and abiotic factors. This would provide useful insight into the effects of a structurally complex homogeneous habitat invaded by *C. odorata* on vegetation composition and ant patterns, interactions and assemblages.

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CHAPTER 3

The effect of grazing on habitat complexity; and how habitat complexity, resources and competition interact to structure local ant assemblages.

Abstract

In savannas, grazing is an important disturbance that modifies the grass layer structure and composition. The structural complexity of a habitat has been shown to affect competition for resources and the assemblage composition of ants. This study investigated the differences in vegetation structure between grazing lawns (areas of intensely grazed patches) and adjacent bunch grass matrices. By using a combination of natural sites and manipulated experiments, I explored how habitat structure affects ant diversity and foraging behaviour, specifically efficiency of resource acquisition, resource monopolisation and ant body size. It was found that ants were faster at locating resources and were more abundant in the grazing lawn habitat and simple treatments than in the bunch grass habitat and more complex treatments. However, the body size of the ants was only affected by the manipulated experiments (fine, coarse, control and bait card) and they were found to be smaller in the more complex treatments than the simple treatments. In both the grazing lawn and bunch grass habitats there were difference in assemblage patterns of ants discovering resources and those dominating them. Grazing thus had a significant effect on ant diversity and foraging behaviour, with dominant ants promoted where habitat complexity was simplified. These results indicate that structural complexity plays an important role in the assemblage patterns and behaviour of its associated fauna.

Introduction

In ecology, determining the factors that govern species diversity, interactions and patterns is a taxing task, but one that is beneficial to the understanding of ecological processes and functioning (Joern, 2005). Habitat structure is one such factor that has been shown to influence faunal behaviour and diversity (e.g. Hurlbert, 2004; Tews *et al.*, 2004; Lassau *et al.*, 2005, Lassau & Hochuli, 2005). Changes have been noted in predatory (Almany, 2004; Grabowski, 2004) and foraging behaviour (Goteceitas & Colgan, 1989; Kelaheer, 2003) as well as competitive interactions (Lassau *et al.*, 2005; Lassau & Hochuli, 2005). A habitat high in structural complexity may reduce predator-prey interactions thus increasing the number of refuge areas due to the presence of interstices (Almany, 2004; Grabowski, 2004). The interstices in turn may exclude certain species of a particular size class, therefore restricting their foraging area and altering competitive interactions (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006). As habitat structural complexity decreases, the species ability to access and locate resources increases. Consequently the number of encounters among species increases, resulting in a highly competitive environment (Gibb & Parr, 2010). As structural complexity plays a significant role in structuring assemblages, disturbances that alter the vegetation will indirectly play a role in structuring ant communities. In savannas grazing is an important disturbance that can significantly influence habitat structural complexity through changes to the grass layer structure (McNaughton, 1985; Archibald *et al.*, 2005).

Grazing plays a vital role in the modification and maintenance of the savanna biome, including the formation of grazing lawns (McNaughton, 1979; McNaughton, 1985; Painter & Belsky, 1993; Cromsigt, 2006). Grazing lawns, patches of short, stoloniferous grasses, are formed when bunch grasses (e.g. *Themeda triandra*, *Eragrostis curvula* and *Hyparrhenia filipendula*) which are less resilient (Coughenour, 1985) to disturbances than grazing lawns are subject to intensive grazing. This intensive grazing of the bunch grasses results in a compositional shift towards more resilient stoloniferous lawn grasses (e.g. *Urochloa mosambicensis*, *Digitaria longifolia*, and *Sporobolus nitens*) (McNaughton, 1985; Archibald *et al.*, 2005; Cromsigt, 2006) which are structurally simple habitats, particularly at ground level (e.g. more bare ground). Gregarious grazing by large ungulates, the presence of fire (McNaughton, 1985; Archibald *et al.*, 2005) and high nutrient availability are all thought to contribute to the formation and preservation of these grazing lawns (Cromsigt, 2006The

presence of grazing lawns adds heterogeneity to the savanna biome, positively influencing the diversity of the ecosystem (Krook *et al.*, 2007; Mgobozi, 2008).

This study aims to determine the effects of changes in habitat structural complexity between grazing lawns and adjacent bunch grass sites on (1) the diversity and composition of ant assemblages, and (2) the ability of ants to locate and capture food resources. Ants occupy several niches within the food chain (generalist predators, scavengers, seed dispersers and competitors) (Andersen, 1995; Sanders & Planter, 2007) and play key roles as ecosystem engineers (nutrient cycling, soil turning and their interactions with biotic factors) (Folgrait, 1998; James, 2004). Recent studies have shown that ants can be sensitive to vegetation structural change within their habitat (Lassau & Hochuli, 2005; Gibb & Parr, 2010).

Specifically, this study aims to investigate how habitat structural complexity affects resource discovery, resource control and ant body size. Theory on species co-existence predicts a trade-off between the ability to discover and the ability to dominate resources (Fellers, 1987; Davidson, 1998; Holway, 1999; Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007; Gibb & Parr, 2010). Because structural simplicity facilitates movement through the environment, we predict resources in the grazing lawn sites will be accessed at a faster rate than those in the bunch grass sites and more baits overall will be discovered. Additionally I will explore whether ant body size changes as a function of habitat complexity. The size-grain hypothesis predicts that the more structurally complex the habitat, the smaller the size of the organism (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006). Therefore it is predicted that the grazing lawn habitat will generally support assemblages of larger ants. This study considers the effects of both natural and manipulated complexities between two different seasons.

Methods

STUDY AREA

Sampling was conducted in Hluhluwe-iMfolozi Park (HiP) which is situated in northern KwaZulu-Natal (between 28°00'S - 28°26'S and 31°43'E - 32°09'E) South Africa (Macdonald, 1983). HiP encompasses a total of 900 km² with a wide variation in altitude and rainfall. For this study sampling was restricted to lower elevations in the iMfolozi section of the park. The majority of the rainfall occurs in the summer between the months of October and March and averages 650 mm in the study area. Average daily temperatures vary between a minimum of 13 °C and a maximum of 35 °C (Cromsigt, 2006). The physiognomy of HiP

may be described as a mesic savanna in the north (Hluhluwe) (Archibald *et al.*, 2005) and a semi-arid savanna in the south (iMfolozi) (Whateley & Porter 1983; Waldram, 2005).

Many of the resident species in the park are grazing mammals, which have increased in total numbers since the area became protected and fenced in 1895. As a result of increased herbivore pressure a number of grazing lawns have been created; these range in size from a 2 m to 6 m in diameter (Mgobozi, 2008). Grazing lawn sites are interspersed with trees, bush and taller bunch grasses (Waldram, 2005). Sampling was carried out on six bunch grass sites (structurally complex habitat) (Figure 3.1a) and six grazing lawn sites (structurally simple habitat) (Figure 3.1b) situated in the northern section of iMfolozi Park.

VEGETATION STRUCTURAL COMPLEXITY AND COMPOSITION

Microhabitat structural complexity was quantified for the two habitat types along an 80 m transect. Where a continuous transect was not possible, multiple shorter transects totalling 80 m were used. The vertical structural complexity of the two habitats was determined by placing a pole vertically on the transect at 8 m intervals. The pole had four 5 x 6 cm laminated cards (each consisting of 20 red dots in a 5 x 4 grid) attached at intervals of 3 cm (essentially ground-level), 15 cm, 30 cm and 50 cm. The number of red dots visible from a horizontal distance of 2 m was recorded.

Every 2 m along the transect the maximum height of grass, forbs and small trees was recorded. The presence or absence of certain habitat components such as bare ground, dung and rocks that were in contact with the pole was also noted. At 8 m intervals the percentage canopy cover was estimated by using a cylinder 4.5 cm in diameter. At every 4 m the distance to the closest tree was also measured (Gibb & Parr, 2010). The surveys of both habitat structure and complexity were conducted in summer (February) and in winter (July) to determine seasonal variation.

The vegetation composition was determined and the communities delineated using the Braun-Blanquet method (Kent & Coker, 1995). A quadrat covering 200 m² was placed in each of the 12 sites, and the percentage cover of each plant species was recorded and classified according to the Braun-Blanquet scale of cover. All major environmental factors, including rock content, aspect, angle of slope, altitude and other factors that might have contributed to the site characteristics were recorded.



Figure 3.1. Photographs depicting (a) the complex bunch grass habitat and, (b) the simple grazing lawn habitat in Hluhluwe-iMfolozi Park.

ANT ASSEMBLAGE DIVERSITY & COMPOSITION: PITFALL TRAPPING

Pitfall trapping was conducted once during the summer (February 2008). At each site, twenty pitfall traps were set up in a rectangular grid (40 m x 30 m) with 10 m spacing between the

traps. Traps were open for 5 days so as to catch a representative proportion of the ant species occurring in that area (Parr & Chown 2001). Each trap was 120 mm deep with a diameter of 52 mm, and was filled with approximately 10 mm of 50/50 water/propylene glycol solution as a preservative (Parr *et al.*, 2002; Parr *et al.*, 2004) and a drop of detergent to reduce surface tension (Netshilaphala, 2005). Once the traps were collected the ants were separated from the rest of the invertebrates caught and stored in vials containing 70% ethanol. Ant specimens were identified to species level in the laboratory.

ANT FORAGING BEHAVIOUR: MANIPULATED TREATMENTS

In addition to the natural habitat comparison, within each habitat a manipulation experiment was set up in order to determine the effect of habitat complexity on ant foraging behaviour. The experimental design was similar to that used by Sarty *et al.*, (2006) and Gibb & Parr (2010). The manipulated treatments were set up in both the complex and simple habitat in all 12 sites. At each site the role of microhabitat complexity was tested using two experimental treatments: “fine” and “coarse” and two control treatments: “control” and “bait card” i.e. a total of four treatment types. There were six replicates of the four treatments (arena) in each site. Experimental treatment arenas were constructed using round transparent plastic containers (14.7 cm in diameter, 12.5 cm in height), containing a central observation chamber (see Sarty *et al.*, 2006). “Control” treatments consisted of containers with no added structure, while “bait card” treatments consisted simply of a card on which the bait was placed. Containers for the “fine” and “coarse” treatments were filled with materials occurring in the surrounding area to create structure. Materials selected consisted of grass and litter in the bunch grass experiments and stones, grass and litter in the grazing lawn experiments. Cotton wool was packed on top of these materials to prevent ants walking over the top of the experimental habitat. Ants were able to access the central chamber through 1 cm circular holes, 1 cm apart, cut into both the observation chambers and the microhabitat chambers. To attract a variety of ants, fish-based protein and honey (carbohydrate) baits were placed within the central chamber. The protein was cut into blocks 1 cm x 1.5 cm and the honey was placed in a small vial lid 2.5 cm in diameter to allow for standardisation. A Petri dish lid was also placed over the central observation chamber to prevent the ants climbing in or out so as to ensure they travelled through the vegetation interstices.

Gap size within the microhabitat arenas was measured by placing a transparency with a regular grid of 16 points over the experimental microhabitat (depth 7 cm), and held over a light source. Gaps closest to each of the 16 points were traced to a transparency and measured

to the nearest 0.5 mm. The average gap size for the bunch grass fine treatment was $0.4 \text{ (SE } \pm 0.215 \text{ mm)}$ and the bunch grass coarse treatment was $2.94 \pm 1.295 \text{ mm}$. The more simple grazing lawn habitat had an average gap size of $0.989 \pm 0.609 \text{ mm}$ in the fine treatment and $3.533 \pm 2.072 \text{ mm}$ in the coarse treatment.

Within each site, six arenas were placed in a randomised 4 m² block design. Arenas were placed roughly 20 m apart. The experiment was started at approximately 08h00 and lasted 3 hours. The temperature at the start of the experiment and every hour afterwards was recorded to account for ant activity as they are sensitive to temperature (Kaspari, 1993). To explore the effect of seasonal variation this experiment was conducted in June and December 2008. Temperatures while sampling in winter ranged from 24.1°C – 32.9°C and 23.9°C – 31.3°C for grazing lawn and bunch grass sites respectively. Summer temperatures were substantially higher: 28.6°C – 36.2°C in bunch grass sites and 25.6°C – 37.5°C in grazing lawn areas. After placement in the field, all replicates were observed consistently until they had been discovered. The time taken until bait was discovered was recorded and the first ant to discover it was collected through the top of the observation chamber using forceps or an aspirator. After the first ant was collected, replicates were observed at hourly intervals for 3 hours and the temperature, the identity of any ant species present and their abundance were recorded. Species that monopolised a resource after 3 hours were considered to be competitively dominant at that resource, even if interference competition was not observed (“Numerical dominance” at baits, Parr *et al.*, 2005; Parr & Gibb, in review). For analyses of dominance at baits, baits with five or more workers of the same species (and with no other species present) were considered to be monopolised. A specimen was taken of each species of ant at the baits so as to be able to accurately identify them in the lab.

In the lab six specimens of each species of ant that arrived first at the baits was taken to determine the size. The body size index (BSI) which is the result of the measurement of the head width x hind femur was then calculated and related to the size-grain hypothesis (Sarty *et al.*, 2006).

DATA ANALYSIS

To quantify the effect of grazing on vegetation complexity and structure, a two-way ANOVA using habitat and season was conducted in the statistical program SPSS version 15.0. Vegetation composition was analysed using the Braun-Blanquet method as well as the software program Plymouth Routines In Multivariate Ecological Research (PRIMER). Data were entered in the form of the Braun-Blanquet cover abundance scale, square root

transformed and then analysed. A one way ANOSIM was conducted, followed by the SIMPER routine to determine the similarities and dissimilarities between the two habitats. To classify plant communities' vegetation composition data were entered into the TURBOVEG software program. The data were then imported into the TWINSpan (a Two-way Indicator Species Analysis) software where a multivariate polithetic clustering algorithm was produced (Kent & Coker, 1995). After refinement was conducted using the Braun-Blanquet procedures a phytosociological table was produced.

To determine if grazing had a significant effect on ant assemblages, data were analysed from the pitfall traps using PRIMER version 6. Raw abundance data were square root transformed to weight appropriately the rare and abundant species (Gibb & Hochuli, 2002). To determine if assemblages of ants differed between the simple and complex habitats a non-metric multidimensional scaling was computed using the Bray-Curtis similarity coefficient. The data were then tested using a two-way Analysis of Similarity (ANOSIM) which produced an R value of between 1 and 0, with one being the most significant and 0 the most insignificant. To establish how much each species contributed to the differences between habitats a SIMPER routine was conducted.

In order to assess the discovery-dominance trade-off theory approximately 10 of the most common species were ranked in terms of their ability to discover resources and ability to dominate resources. A rank of one was given to those species that dominated the resources the most and those that located the food the fastest. A score of eight was given to the species that took the longest to locate resources and dominated the baits the least (Fellers, 1987, Santini, *et al.*, 2007, Parr & Gibb, 2009). The data of assemblages from the complex and simple habitats were analysed both separately and together. Data were all square root transformed and using the Bray-Curtis similarity, a two-way ANOSIM was conducted to determine if assemblages of discoverers differed from the assemblages of dominants within the two seasons and two habitats. A SIMPER routine was consequently carried out to determine how much each species contributed to the differences and similarities between the discoverers and dominants, habitats and seasons (French & Major, 2001; Gibb & Hochuli, 2002).

A three factor ANOVA model was used to analyse the effects of season and habitat structural complexity (manipulated and natural treatments) on the speed of resource discovery, the number of times baits were monopolised and ant species body size. If the ANOVA results proved significant a Kruskal-Wallis test was then conducted to distinguish either the order in which the species of ants arrived at resources, the frequency at which they

monopolised the baits, or to determine the size class of the species. Tukey's HSD post-hoc tests were then conducted to determine which treatments were significantly different.

Results

VEGETATION STRUCTURAL COMPLEXITY AND COMPOSITION

Analysis of the two habitats confirmed that grazing alters the complexity of the vegetation, simplifying it considerably in grazing lawn sites. There were significantly more dots visible at 3 cm, 15 cm and at 30 cm in grazing lawn sites compared to bunch grass sites (Table 3.1). Vertical habitat complexity, as indicated by the visible dots, did not vary between seasons (Table 3.1).

The bunch grass habitat consisted of significantly taller grass species than the grazing lawn habitat (Table 3.1). Small woody species and litter were also significantly more abundant in the bunch grass habitat, emphasising its more complex structure. Importantly there was more ground that was bare in the grazing lawn habitat than in the bunch grass one signifying a more planar environment; this also varied with season with less ground cover in the winter (Table 3.1).

There was a clear distinction between the bunch grass and the grazing lawn habitats in vegetation composition (ANOSIM, Global $R = 0.476$, $P = 0.0002$). The grazing lawn habitat was dominated by the grass species *Urochloa mosambicensis* and *Sporobolus nitens* while the bunch grass habitat was dominated by *Themeda triandra* but also consists of a high percentage contribution of a number of other grass species. A Braun-Blanquet analysis substantiates this evidence and places the 12 relevés (sites) in 3 communities (Table 3.2).

PLANT COMMUNITIES:

1. Community 1 consists of 5 relevés from two sub-communities. These two sub-communities are both located in the grazing lawn habitat of the iMfolozi section in the park. Sub-community 1.1 is situated further away from sub-community 1.2, all with similar gently undulating slopes and sandy soils. The diagnostic species that separate it from communities 2 and 3 is the grass *Sporobolus nitens* and the forb *Aframomum corrorima*. The dominant species include the grass *Urochloa mosambicensis* and the forbs *Justicia flava* and *Blepharis procumbens* (Table 3.2).

Table 3.1a. The comparison of the mean number of visible dots at 3 cm, 15 cm, 30 cm and 50 cm; mean height of forbs, small woody trees and grass; mean number of points where dung, litter and bare ground was present; the distance to the closest tree and percentage canopy cover in the bunch grass habitat and the grazing lawn habitat.

	Bunch Grass (Complex)	Grazing Lawn (Simple)	F _(1,10)	P - value
<i>Mean number</i>				
<i>of visible dots</i>				
3 cm	1.16 (±1.84)	9.91 (±3.62)	54.93	0
15 cm	6.52 (±4.05)	18.98 (±1.37)	104.09	0
30 cm	14.68 (±3.84)	19.56 (±0.87)	18.96	0
50 cm	19.16 (±1.77)	19.96 (±0.14)	2.34	0.14
<i>Mean height (cm)</i>				
Forb	0.02 (±0.04)	0.01 (±0.01)	0.56	0.46
Small woody	0.04 (±0.03)	0.00 (±0.02)	11.3	0
Grass	0.16 (±0.06)	0.01 (±0.01)	85.62	0
<i>Mean number of points where each was present</i>				
Dung	0.75 (±1.60)	0.75 (±1.49)	0	1
Litter	5.67 (±8.12)	1.25 (±3.75)	4.84	0.04
Bare Ground	17.33 (±11.01)	24 (±7.41)	5.8	0.03
Distance to closest tree (m)	3.01 (±2.98)	3.24 (±2.33)	0.04	0.84
% canopy cover	9.09 (±7.98)	6.14 (±5.58)	1.17	0.29

Table 3.1b. The comparison of the mean number of visible dots at 3 cm, 15 cm, 30 cm and 50 cm; mean height of forbs, small woody trees and grass; mean number of points where dung, litter and bare ground was present; the distance to the closest tree and percentage canopy cover in the summer and winter seasons.

	Summer	Winter	F _(1,10)	P - value
<i>Mean number of visible dots</i>				
3 cm	5.15 (±5.15)	5.92 (±5.61)	0.42	0.52
15 cm	13.18 (±6.74)	12.33 (±7.56)	0.48	0.5
30 cm	17.49 (±2.85)	16.74 (±4.48)	0.45	0.51
50 cm	19.74 (±1.78)	19.38 (±1.78)	0.49	0.49
<i>Mean height (cm)</i>				
Forb	0.02 (±0.04)	0.01 (±0.01)	0.64	0.43
Small woody	0.02 (±0.03)	0.03 (±0.04)	0.1	0.76
Grass	0.07 (±0.07)	0.1 (±0.1)	2.55	0.12
<i>Mean number of points where each was present</i>				
Dung	0.00 (±0.00)	1.5 (±1.88)	6.92	0.02
Litter	0.17 (±0.58)	6.75 (±8.16)	10.76	0
Bare Ground	14.33 (±7.19)	27.00 (±7.82)	20.93	0
Distance to closest tree (m)	2.87 (±2.94)	3.38 (±2.36)	0.21	0.65
% canopy cover	10 (±5.87)	5.23 (±7.26)	3.05	0.1

1.1. The three relevés, 9, 10 and 11, of this sub-community, are the grazing lawn sites 4, 5 and 6. They all occur between 256 m and 123 m above sea level with a slope angle of between 2° and 3°. Relevés 9, 10 and 11 were facing the north-west, west and north respectively, while all their slopes were between 2° and 3°. The diagnostic species of these relevés included species from species group A. These diagnostic species include the tree species *Maytenus heterophylla*, and the forb species *Deiosperma ashtonii*, *Commelina erecta*, *Boerhavia* spp. and *Tragia* spp.. The dominant species are the grasses *Sporobolus nitens* and *Urochloa mosambicensis* and the forbs *Justicia flava*, *Blepharis procumbens* and the *Ruellia* species (Table 3.2).

1.2. The relevés 7 and 12 are the grazing lawn sites 1 and 6 and are relatively close to the Black iMfolozi River. They are between 140 m and 123 m above sea level with both slopes less than 2°, facing north west and north respectively. Species group B contains the diagnostic species from these relevés. Some of the species include the trees *Acacia karoo* and *Acacia nilotica*, the grass *Dactyloctenium australe* and the forbs *Schizanthus pinnatus* and *Tribulus terrestris*. The dominant species include the grasses *Sporobolus nitens*, *Urochloa mosambicensis* and *Panicum maximum*, and the forbs *Justicia flava* and *Blepharis procumbens* (Table 3.2).

2. Community 2 consists of relevés 3, 4 and 5 which also demarcate the bunch grass sites 3, 4 and 5. These sites are located in a similar area within the bunch grass habitat between 229 m and 254 m above sea level. Each of these sites is on a relatively flat area with slopes between 1° and 3°. The soil was composed of less sand than that of the grazing lawn sites. Group D contains the diagnostic species for this community. These species include the trees *Acacia karoo*, *Acacia gerrardii*, *Spirostachys africanum* and *Rhus pentheri* and the grasses *Dactyloctenium giganteum*, *Eragrostis curvula* and *Panicum deustum* and the forbs *Indigofera confuse*, *Crabbea hirsuta* and *Asparagus multiflorus*. The dominant species include the trees *Ehretia rigida* and *Dichrostachys cinerea*, the grasses *Digitaria eriantha*, *Bothriochloa insculpta*, *Themeda triander* and *Panicum maximum* and the forbs *Justicia flava* and *Blepharis procumbens* (Table 3.2).

3. Community 3 constitutes four relevés, (1, 2, 6 and 8), three occurring in the bunch grass habitat (1, 2 and 6) and one occurring in the grazing lawn habitat (8). Relevés 1, 2 and 6 from the bunch grass habitat (sites 1, 2 and 6) were located in a similar area between 122 m and 159 m above sea level. Relevés 1 and 2 were located on a gently sloping north-facing area with slopes of between 2° and 4°, covered 2% by fist sized rocks and 10% by large

rocks. Although relevé 6 was located further away from relevés 1 and 2 (which were in close proximity to each other), the slope was still north facing. In this community the only site located in the grazing lawn habitat had a north-facing slope of 2°. This relevé was situated very close to the Black iMfolozi, so received much run-off during the rainy season and was heavily impacted by grazing. The diagnostic species include the trees *Grewia caffra*, *Spirostachys africana*, and *Acacia grandicornuta*, the grass *Arista congesta* and the forbs *Lippia javanica*, *Polygala rehmannii* and *Barleria gueinzii* (species group G). The dominant species of this community are the grasses *Eragrostis superba*, *Bothriochloa insculpta* and *Themeda triandra* and the forb *Heliotropium steudneri* (Table 3.2).

Plant species richness differed between the two habitats, with the bunch grass habitat exhibiting 79 species, and the grazing lawn habitat only 58. The bunch grass habitat exhibited a higher number of grass species (Bunch grass: 12; Grazing lawn: 8) and tree species (Bunch grass: 29; Grazing lawn: 16), while forb species numbers remained similar for both habitats (34 species each). There appears to be no significant correlation between ant species richness and plant species richness.

ANT ASSEMBLAGE DIVERSITY & COMPOSITION

A total of 57 species was recorded with 40 from the grazing lawn sites and 48 from the bunch grass sites. There was no significant difference between abundance and habitat ($P = 2.048$) or species richness and habitat ($P = 0.388$). Ant assemblage composition differed significantly between the grazing lawn and the bunch grass habitats (Global $R = 0.4$, $P = 0.004$) (Figure 3.2). The top four species that contributed to 53.62% of the dissimilarity of the two habitats are *Anoplolepis custodiens* (12.07 %), *Myrmecaria natalensis* (5.06%), *Pheidole* species A (4.58) and *Pheidole* species H (4.03).

RESOURCE DISCOVERY AND MONOPOLISATION

Speed of bait discovery

The number of baits discovered increased significantly with time in both the bunch grass habitat ($F_{(2, 30)} = 13.84$, $P < 0.0001$) and grazing lawn habitat ($F_{(2, 30)} = 6.45$, $P = 0.05$). After 180 min there was no significant difference between baits discovered, habitat ($F_{(1,20)} = 3.45$, $P = 0.08$) and season ($F_{(1,20)} = 1.13$, $P = 0.30$). There were more baits discovered and occupied in summer than winter in the bunch grass habitat. The grazing lawn habitat showed very little difference between seasons except at 60 min where baits were discovered faster in summer than winter (Table 3.3).

Table 3.2. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the grazing lawn and bunch grass habitats.

Community Number	1			2			3					
	1.1		1.2									
Relevé Number	9	10	11	7	12	3	4	5	1	2	6	8
Species Group A												
<i>Boerhavia species</i>	a		A									
<i>Delosperma ashtonii</i>	1	1										
<i>Commelina erecta</i>			1 1									
<i>Hibiscus calyphyllus</i>	1		+									
<i>Tragia species</i>			1 +									
<i>Kyphocarpa angustifoli</i>	1											
<i>Maytenus heterophylla</i>		+										
<i>Tragus berteronianus</i>			1									
<i>Acrotome hispida</i>			+									
<i>Asparagus ramosissimus</i>			1									
<i>Chloris virgata</i>			+									
Species Group B												
<i>Schizanthus pinnatus</i>				a	a							
<i>Gomphrena celosioides</i>					a							
<i>Dactylocteni austral</i>					4							
<i>Tribulus terrestris</i>					3							
<i>Portulaca kermesina</i>				+								
<i>Acacia karroo</i>					1							
<i>Acacia nilotica</i>					1							
<i>Sida dregei</i>					1							
<i>Indigofera longibarbat</i>					1							
Species Group C												
<i>Sporobolus nitens</i>	a	a	A	a	a							
<i>Aframomum corrorima</i>	3		A		1							
Species Group D												
<i>Rhus pentheri</i>						+	+	+				
<i>Crabbea hirsuta</i>						3		3				
<i>Dactylocteni giganteum</i>						a	+					
<i>Eragrostis curvula</i>						1	1					
<i>Gerbera viridifolia</i>						+	1					
<i>Acacia karroo</i>						+		1				
<i>Indigofera confusa</i>						1		1				
<i>Cymbopogon excavatus</i>						a						
<i>Hypericum forrestii</i>						1						
<i>Acacia gerrardii</i>						+						

Table 3.2 Continued. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the grazing lawn and bunch grass habitats.

Community Number	1			2		3			
	1			1					
Relevé Number	9	10	11	7	12	3	4	5	1 2 6 8
Species Group D continued									
<i>Acacia karroo</i>							1		
<i>Stylochiton natalensis</i>							+		
<i>Hibiscus species</i>							+		
<i>Panicum deustum</i>							+		
<i>Maytenus species</i>							+		
<i>Spirostachys africana</i>							+		
<i>Euclea divinorum</i>								1	
<i>Ziziphus mucronata</i>								1	
<i>Setaria sphacelata</i>								1	
<i>Asparagus multiflorus</i>								1	
<i>Grewia species</i>								+	
<i>Schotia brachypetala</i>								+	
<i>Maytenus mossambicens</i>								+	
Species Group E									
<i>Capparis tomentosa</i>				+		+		+	
<i>Plectroniella armata</i>				1			+		
<i>Euclea divinorum</i>				1			+		
Species Group F									
<i>Acacia tortilis</i>			1					1	
<i>Acacia nilotica</i>			+					+	
<i>Rhoicissus tridentata</i>			+					+	
<i>Crassula sediflora</i>		1	1			1	1		
<i>Barleria prionitis</i>		+				a		1	
<i>Acacia tortilis</i>		a		a		1	1		
<i>Ocimum americ v. ameri</i>	1		1		1	a	1	1	
<i>Hypoestes forskoolii</i>	+			+				1	
Species Group G									
<i>Aristida congesta</i>									+ 1 a
<i>Indigofera longebarbat</i>									1 1
<i>Grewia caffra</i>									+ 1
<i>Commiphora schimperi</i>									+ 1
<i>Elaeodendro transvaale</i>									+ +
<i>Spirostachys africana</i>									+ +
<i>Acacia grandicornuta</i>									a
<i>Acrostemon stokoei</i>									+ +
<i>Lippia javanica</i>									+ +
<i>Acrotome species</i>									1

Table 3.2 Continued. A Braun-Blanquet phytosociological table of the plant species occurring within the 12 relevés of the grazing lawn and bunch grass habitats.

Community Number	1						2			3			
	1.1			1.2									
Relevé Number	9	10	11	7	12		3	4	5	1	2	6	8
Species Group G continued													
<i>Grewia villosa</i>										1			
<i>Polygala rehmannii</i>										1			
<i>Melhania forbesii</i>										+			
<i>Aerva leucura</i>												1	
<i>Barleria gueinzii</i>												1	
<i>Grewia caffra</i>												+	
<i>Spirostachys africana</i>												+	
Species Group H													
<i>Acacia nilotica</i>							+	1		1		+	
<i>Digitaria eriantha</i>							a	1	a	1		a	
<i>Chascanum hederaceum</i>							+		+		a		
<i>Euclea racemosa</i>							+	+	+			+	
<i>Bothriochloa insculpta</i>							1	1	a	1	3	4	
Species Group I													
<i>Pavonia burchellii</i>				3	+					a			
<i>Grewia villosa</i>				+	+							+	
<i>Indigofera species</i>					a						+	+	+
<i>Boerhavia diffusa</i>				a									a
<i>Maytenus heterophylla</i>					1	+				+			
<i>Eragrostis superba</i>					1	a				a	1	1	1
<i>Acacia nigrescens</i>					1					a	a	1	
<i>Themeda triandra</i>					1	a	a	1		3	4	1	
Species Group J													
<i>Justicia flava</i>	3	a	a	3	4		3	a	a	1		1	
<i>Ruellia species</i>	1	a	a				1	3	1			a	
<i>Blepharis procumbens</i>	a	1	3	3	3			a				a	
<i>Urochloa mosambicensis</i>	a	a	3	a	a			1	1				a
<i>Dichrostachys cinerea</i>		+	+	+			+	1	+	+		+	
<i>Panicum maximum</i>			1	a	3		1	3	1	1		1	
<i>Panicum coloratum</i>		a		1	1		1	a		1		a	
<i>Phyllanthus pentandrus</i>		1		1	1		1	1	1		+	a	
<i>Heliotropium steudneri</i>		a		1				1			a	+	+
<i>Ehretia rigida</i>	+				+		1	4	+	+	1	1	
<i>Hibiscus trionum</i>			a	1	1					a			
<i>Evolvulus alsinoides</i>		1	1						1	1			
<i>Solanum panduriforme</i>	+		+		a							+	
<i>Sida alba</i>		1	+				+		1		3		
<i>Acacia tortilis</i>	+												+

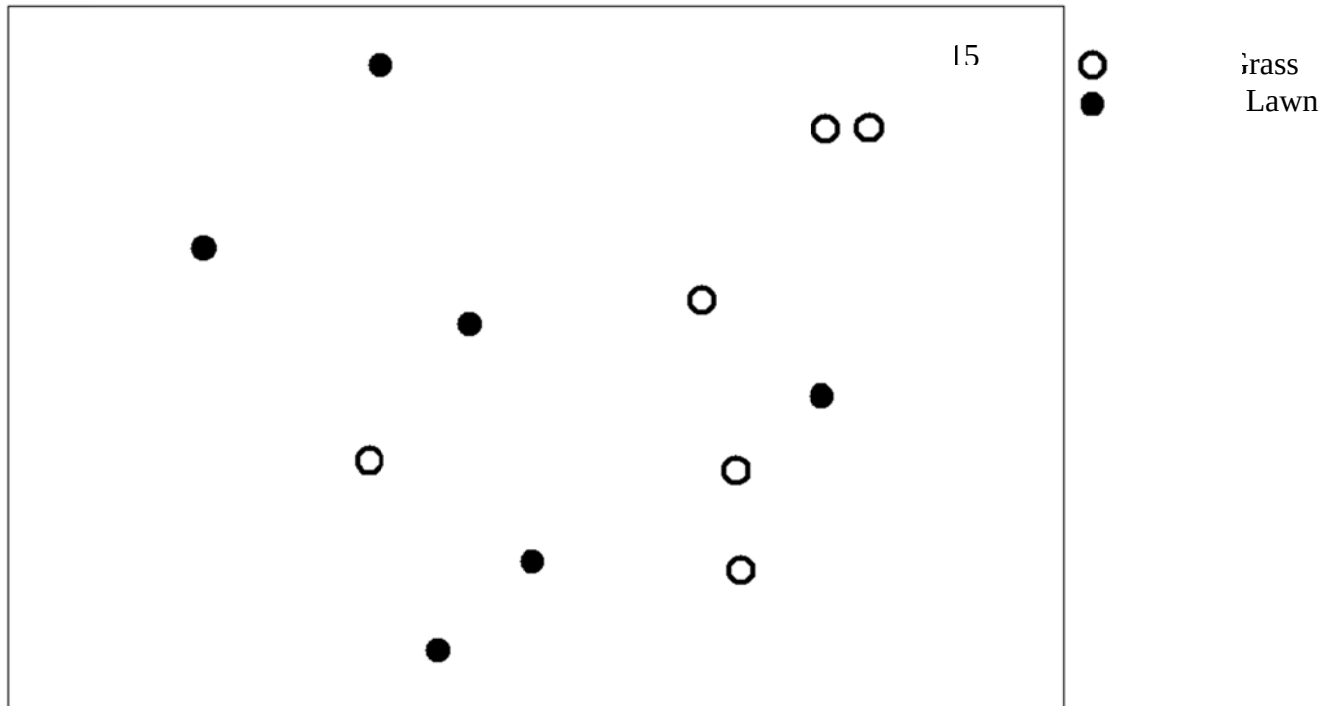


Figure 3.2. Non-metric multidimensional scaling ordination for bunch grass and grazing lawn ant assemblages. R value = 0.4 and P value = 0.0004.

Table 3.3. Mean number of baits occupied in the bunch grass habitat and the grazing lawn habitat for the summer and winter season over a 180 minute period. $\pm$ is standard deviation.

	Bunch Grass		Grazing Lawn	
	Summer	Winter	Summer	Winter
Mean number of baits occupied				
60 min	13.00 (± 4.05)	11.7 (± 3.60)	19.50 (± 4.32)	14.67 (± 3.72)
120 min	16.50 (± 4.18)	15.50 (± 5.32)	18.67 (± 5.61)	19.83 (± 2.93)
180 min	21.17 (± 3.06)	19.83 (± 2.79)	22.83 (± 1.83)	22.00 (± 2.10)

The effect of habitat, treatment and season on time of resource discovery was examined by using a three factor full model ANOVA which revealed significant differences. With the natural experiments (data for summer and winter combined) results showed that overall ants were faster at discovering the baits in the less complex grazing lawns than in the bunch grass habitat (ANOVA, $F_{(1,80)} = 12.55$, $P = 0.001$, mean $\pm$ SE = 48.8minutes $\pm$ 32.8 and 68.6 $\pm$ 41.6 for grazing lawn and bunch grass respectively). There was also a seasonal effect with ants in the winter being slower to reach the baits than in summer ($F_{(1,80)} = 16.820$, $P < .0001$, see also Figure 3.3a).

In both the grazing lawn habitat and bunch grass habitat there were significant differences between the manipulated treatments in the speed of resource discovery (Grazing lawn habitat, $F_{(3,40)} = 9.74$, $P < 0.0001$; Bunch grass habitat, $F_{(3,40)} = 14.98$, $P < 0.0001$). A Kruskal- Wallis test revealed that the open bait card was discovered first (mean time of 19.64 $\pm$ 13.03 min in the grazing lawn habitat and 29.24 $\pm$ 13.73 min in the bunch grass habitat), followed by the control (41.25 $\pm$ 23.03 min in the grazing lawn habitat and 61.63 $\pm$ 29.14 min in the bunch grass habitat) in both the bunch grass habitat (Figure 3.3b) and grazing lawn habitat (Figure 3.3c). In the bunch grass habitat the coarse treatments were discovered next (75.86 $\pm$ 37.71 min) and then fine treatments (107.71 $\pm$ 38.08 min). The discovery rate for the coarse (68.86 $\pm$ 29.10 min) and fine (65.44 $\pm$ 36.48 min) treatments were inversed in the grazing lawn habitat. Tukey's *post-hoc* tests revealed that the bait card was discovered significantly faster than the control, coarse and fine treatments in the bunch grass habitat. There was no significant difference between the control and coarse treatments and the control and bait card treatments. In the grazing lawn habitat the bait card was discovered at a significantly faster rate than the coarse and fine treatments (Figure 3.3c).

Resource monopolisation

In grazing lawn sites, the percentage of baits monopolised at 60 min was higher than in the bunch grass habitat (Table 3.3); these values increased over time, staying higher in grazing lawn sites. Although overall monopolisation was higher in grazing lawns in the summer, the percentage monopolised baits decreased continuously in the grazing lawn habitat; this trend was not as clear on bunch grass sites (Table 3.4).

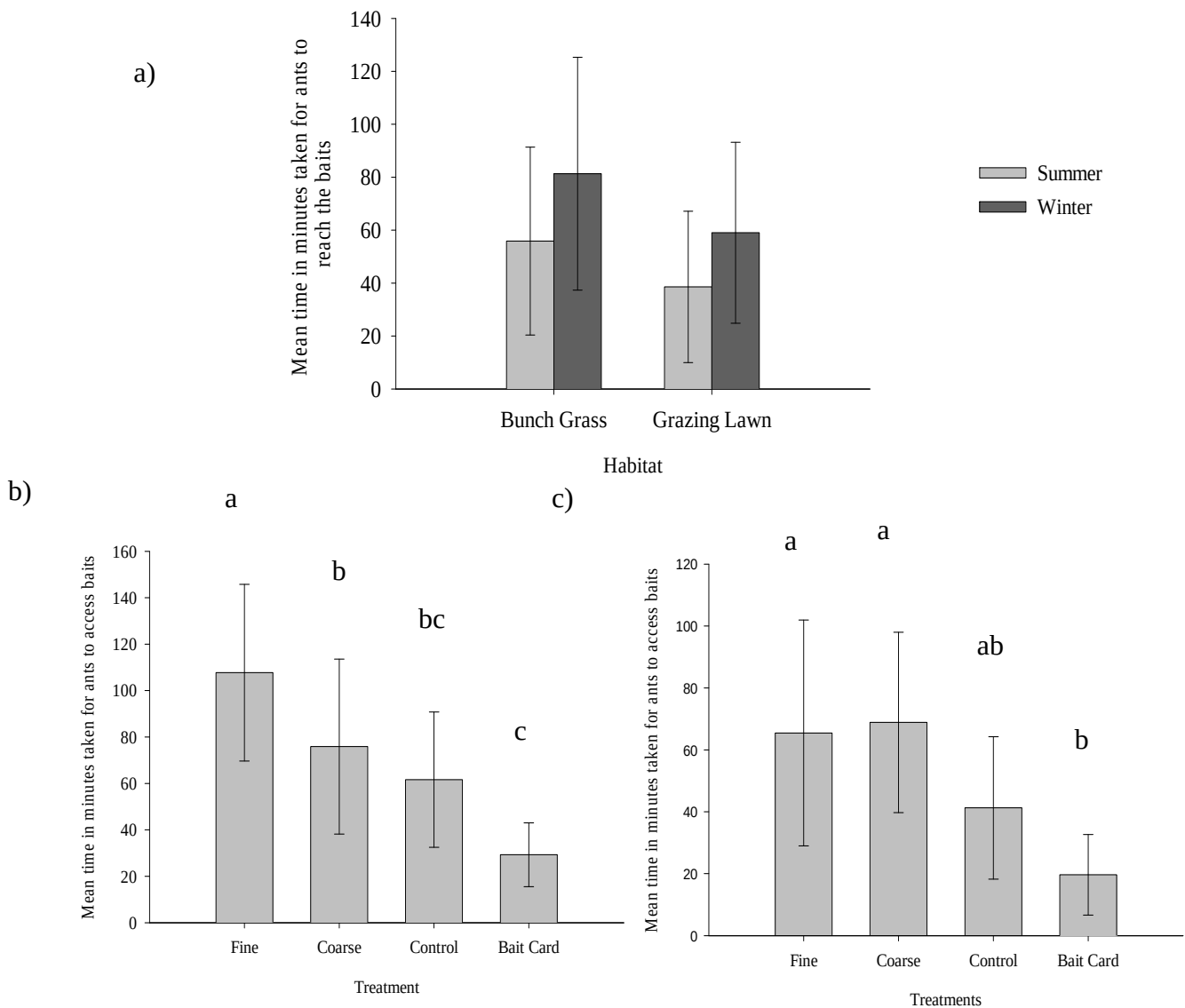


Figure 3.3. Mean (SE) time for ants to discover baits when comparing season a) in the natural habitats and b) the complex bunch grass habitat and simple grazing lawn habitat with the manipulated treatments. Bars with different letters are significantly different.

Table 3.4. Percentage of baits monopolised in the bunch grass habitat and the grazing lawn habitat for the summer and winter season over a 180 minute period.

Time in minutes	Bunch Grass		Grazing Lawn	
	Summer	Winter	Summer	Winter
60	38.19	38.19	66.67	47.22
120	45.83	50.69	59.03	66.67
180	36.81	59.02	52.08	68.75

The number of monopolised baits in the natural experiment was significantly different between habitats (ANOVA $F_{(1,80)} = 19.45$, $P < 0.0001$). The grazing lawn habitat had a higher mean number of baits monopolised (4.10 ± 1.13) than the bunch grass habitat (2.94 ± 1.66). Season also had a significant impact on the number of monopolised baits within the two habitats (ANOVA, $F_{(1,80)} = 4.19$, $P = 0.04$) with a higher number of ants monopolising baits in winter (3.94 ± 1.42) than in summer (3.10 ± 1.53) (Figure 3.4a). Analysis of monopolisation frequency at the four experimental treatments in the summer and winter seasons combined revealed that there were significant differences between them in the bunch grass habitat (ANOVA $F_{(3,40)} = 3.639$, $P = 0.021$) but not the grazing lawn habitat (ANOVA $F_{(3,40)} = 0.763$, $P = 0.521$). Tukey's *post-hoc* tests indicated that in the bunch grass habitat (Figure 3.4b) the bait card treatment had a significantly higher frequency of ants at the resources than the fine and coarse treatments. The control, however, had ants monopolising the resources at a similar frequency to bait card, coarse and fine treatments (Figure 3.4b). The grazing lawn results indicated no significant difference between any of the treatments when Tukey's *post-hoc* tests were carried out (Figure 3.4c).

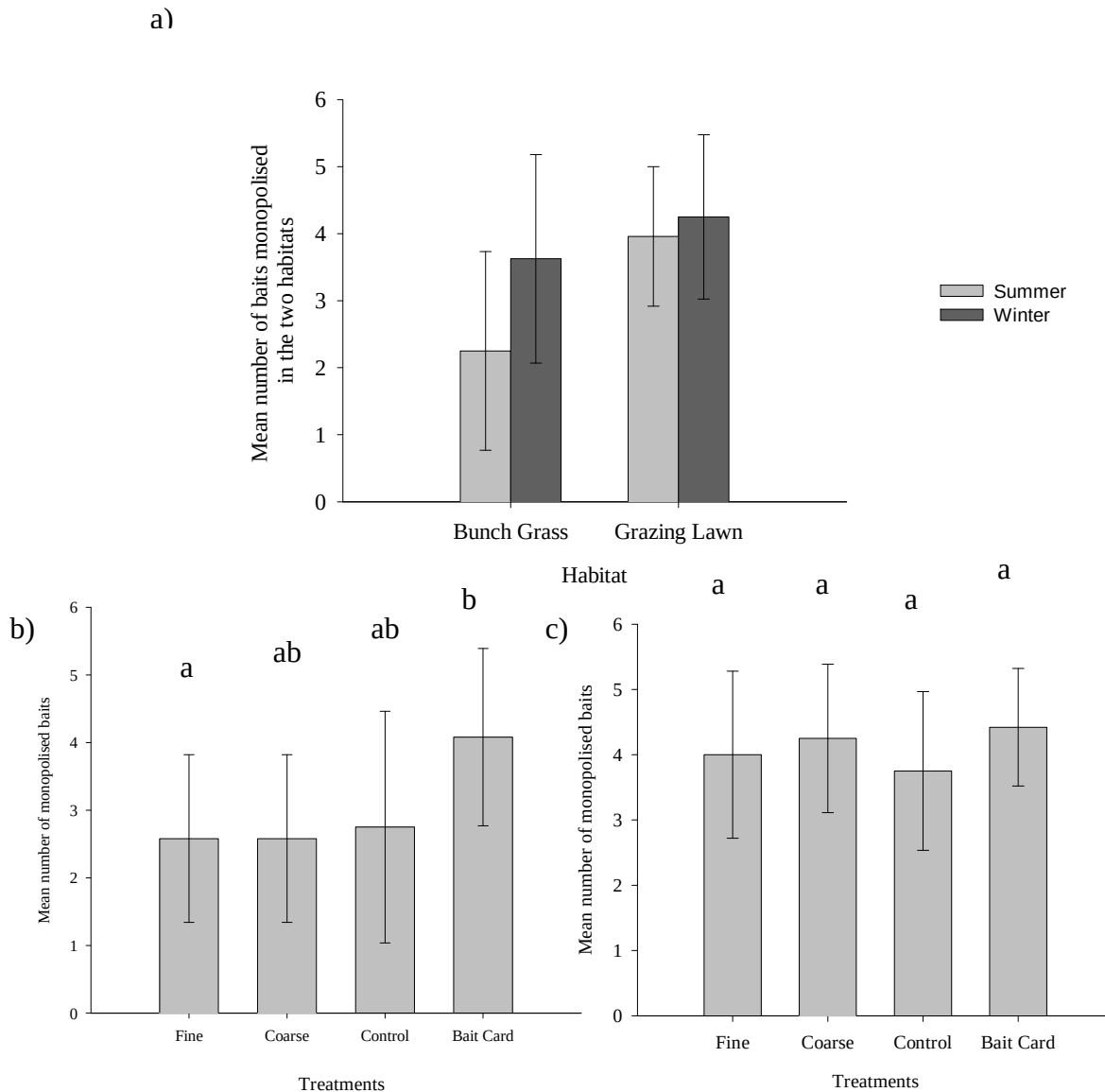


Figure 3.4. Mean (SE) number of ants accessing resources during the summer and winter periods in a) the natural complex bunch grass habitat and the natural simple grazing lawn habitat and in b) the manipulated fine, coarse, control and bait card treatments. Bars with dissimilar letters are significantly different.

Discovery-dominance relationship

A two-way ANOSIM was conducted in which the assemblages were examined between two habitats revealing a significant difference (Discovery versus dominants, Global $R = 0.339$, $P = 0.002$; Habitats Global $R = 0.864$, $P = 0.001$). This implies that the assemblages of

discoverers and dominant ants across the grazing lawn and bunch grass habitats are significantly different. The two-way SIMPER routine indicated that the dominants were made up of mainly three contributors, *Monomorium delagoense*, *Anoplolepis custodiens* and *Pheidole* species G (Table 3.5). *Monomorium delagoense*, *Pheidole* species N, *Monomorium* Species D and *Pheidole* species A, although they did not have very high contributing similarity values, were the most abundant ants recorded first at the resources (Table 3.5). When the habitats were looked at separately, it was also revealed that there was a significant difference between those discovering resources and those dominating resources in the bunch grass habitat and grazing lawn habitat. When the species were ranked the discovery-dominance plot indicated that there was a positive relationship between discoverers and dominants for both the bunch grass habitat (Figure 3.5a) and grazing lawn habitat (Figure 3.5b), and well as both habitats combined (Figure 3.5c).

THE EFFECT OF HABITAT STRUCTURE ON BODY SIZE INDEX

A three factor full model ANOVA yielded an insignificant result ($F_{(1,80)} = 0.169$, $P = 0.682$) for the interaction between BSI and habitat (mean body size $\pm$ SE: 1.01 ± 0.97 and 0.95 ± 0.69 for the bunch grass and grazing lawn habitats respectively). Overall, the mean BSI of the ants recorded in summer was larger (1.27 ± 0.93), whereas the ants recorded in winter were significantly smaller (0.70 ± 0.62 ; ANOVA $F_{(1,80)} = 15.553$, $P < 0.0001$) (Figures 3.6a, 3.7a, & 3.7b).

In accordance with predictions there was a significant difference between the BSI of the ants between the four manipulated treatments ($F_{(3,80)} = 7.06$, $P < 0.001$). The mean BSI (seasons combined) decreased from the bait card (1.51 ± 1.16) to the control (1.04 ± 0.86), then coarse (0.71 ± 0.48) and finally the smallest from the fine treatment (0.68 ± 0.32). The same trend occurred in the bunch grass habitat (ANOVA $F_{(1,40)} = 5.253$, $P = 0.004$) but not the grazing lawn habitat (ANOVA $F_{(1,40)} = 2.026$, $P = 0.126$) when each was examined separately. Tukey's post-hoc tests revealed that the bait card treatment (1.76 ± 1.41) was significantly different from the coarse (0.58 ± 0.27) and fine (0.66 ± 0.36) treatments. The control (1.05 ± 0.91) treatment, however, remained similar to the bait, coarse and fine treatments in the bunch grass habitat (Figure 3.6b). The four treatments in the grazing lawn habitat were not significantly different from each other. The ant BSI ranged from $1.25 (\pm 0.83)$ in the bait card treatment to $1.04 (\pm 0.84)$ in the control treatment, $0.83 (\pm 0.61)$ in the coarse treatment and $0.70 (\pm 0.29)$ in the fine treatment (Figure 3.6c).

Table 3.5. A two way SIMPER routine indicating the characteristic species of ants discovering resources and ants dominating resources in the bunch grass habitat and the grazing lawn habitat.

Ant species per habitat and season	Average abundance of total	Average similarity of total	% contribution to similarity among level
Discoverers (Average similarity 59.01)			
<i>Monomorium delagoense</i>	2.23	8.84	14.98
<i>Pheidole</i> Sp. N	1.55	5.99	10.16
<i>Camponotus cintellus</i>	1.47	5.34	9.06
<i>Monomorium</i> Sp. D	1.58	5.34	9.06
<i>Pheidole</i> Sp. L	0.87	3.86	6.55
<i>Pheidole</i> Sp. G	1.44	3.84	6.51
<i>Monomorium</i> Sp. J	1.06	2.94	4.97
<i>Monomorium</i> Sp. A	0.86	2.75	4.67
<i>Anoplolepis custodiens</i>	1.2	2.65	4.5
<i>Monomorium</i> Sp. K	0.8	2.65	4.5
<i>Tetramorium sericerventre</i>	0.94	2.65	4.5
<i>Pheidole</i> Sp. A	0.64	2.23	3.78
Dominants (Average similarity 58.92)			
<i>Monomorium delagoense</i>	2.34	15.88	26.95
<i>Anoplolepis custodiens</i>	1.74	11.24	19.08
<i>Pheidole</i> Sp. G	1.39	6.75	11.45
<i>Monomorium</i> Sp. A	0.86	5.13	8.7
<i>Pheidole</i> Sp. L	0.68	4.56	7.74
<i>Pheidole</i> Sp. A	0.97	4.31	7.32
Bunch Grass (Average similarity 53.88)			
<i>Monomorium delagoense</i>	1.92	10.66	19.79
<i>Pheidole</i> Sp. G	2.28	10.59	19.66
<i>Monomorium</i> Sp. A	1.72	7.88	14.62
<i>Anoplolepis custodiens</i>	1.02	4.31	8
<i>Pheidole</i> Sp. A	0.67	4.31	8
<i>Camponotus cintellus</i>	0.76	2.19	4.06
<i>Monomorium</i> Sp. C	0.9	2.19	4.06
<i>Monomorium</i> Sp. D	1.13	2.19	4.06
Grazing Lawn (Average similarity 64.06)			
<i>Monomorium delagoense</i>	2.64	14.05	21.94
<i>Anoplolepis custodiens</i>	1.92	9.59	14.97
<i>Pheidole</i> Sp. L	1.55	8.43	13.15
<i>Pheidole</i> Sp. N	1.68	8.27	12.92
<i>Monomorium</i> Sp. D	1.43	6.62	10.34
<i>Camponotus</i> Sp. A	0.5	3.47	5.41
<i>Camponotus cintellus</i>	0.96	3.15	4.92

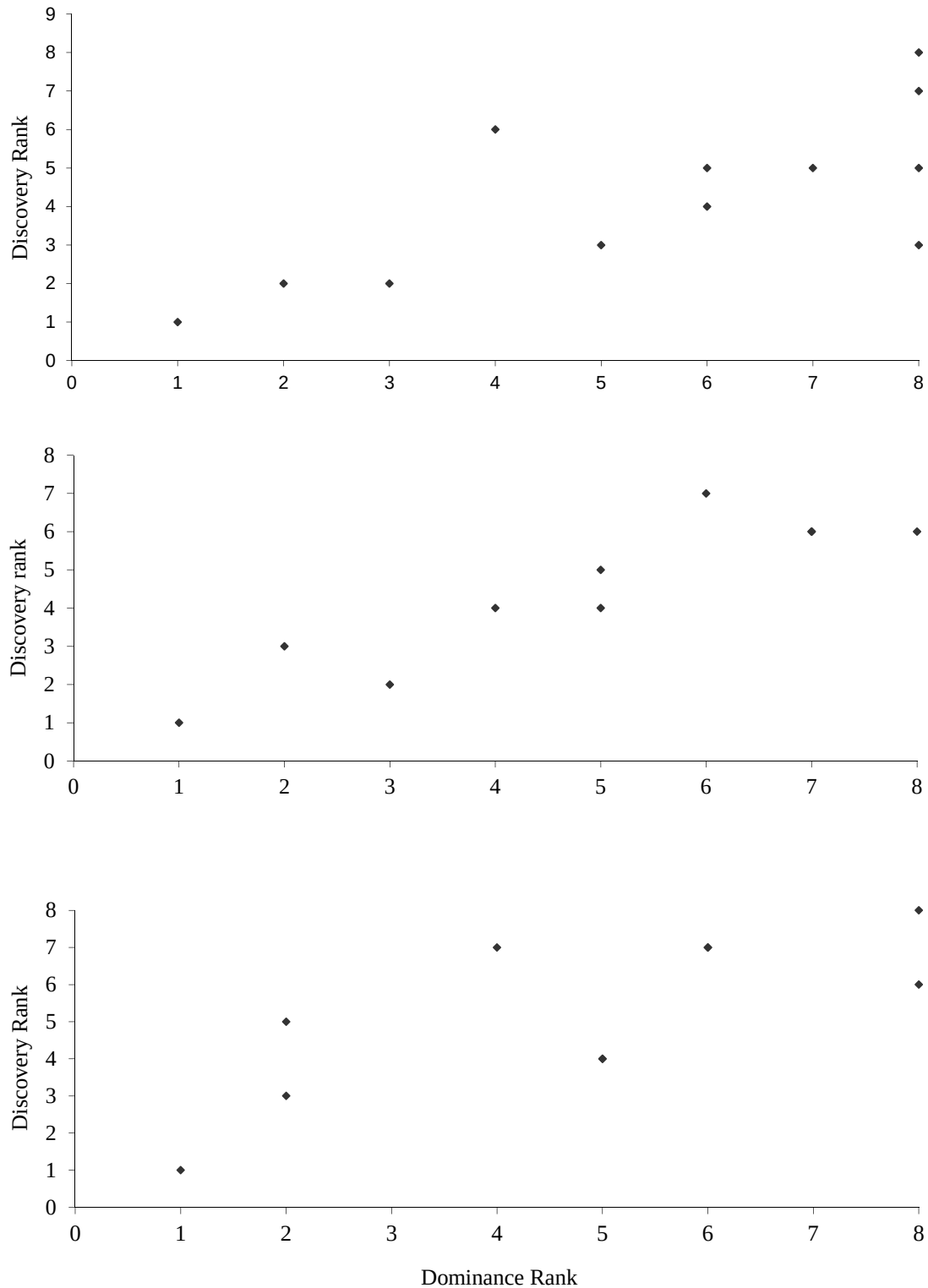


Figure 3.5. Frequency of the ranked ants discovering resources and the ranked ants dominating them in the a) bunch grass habitat, b) grazing lawn habitat and, c) the bunch grass and grazing lawn habitats combined.

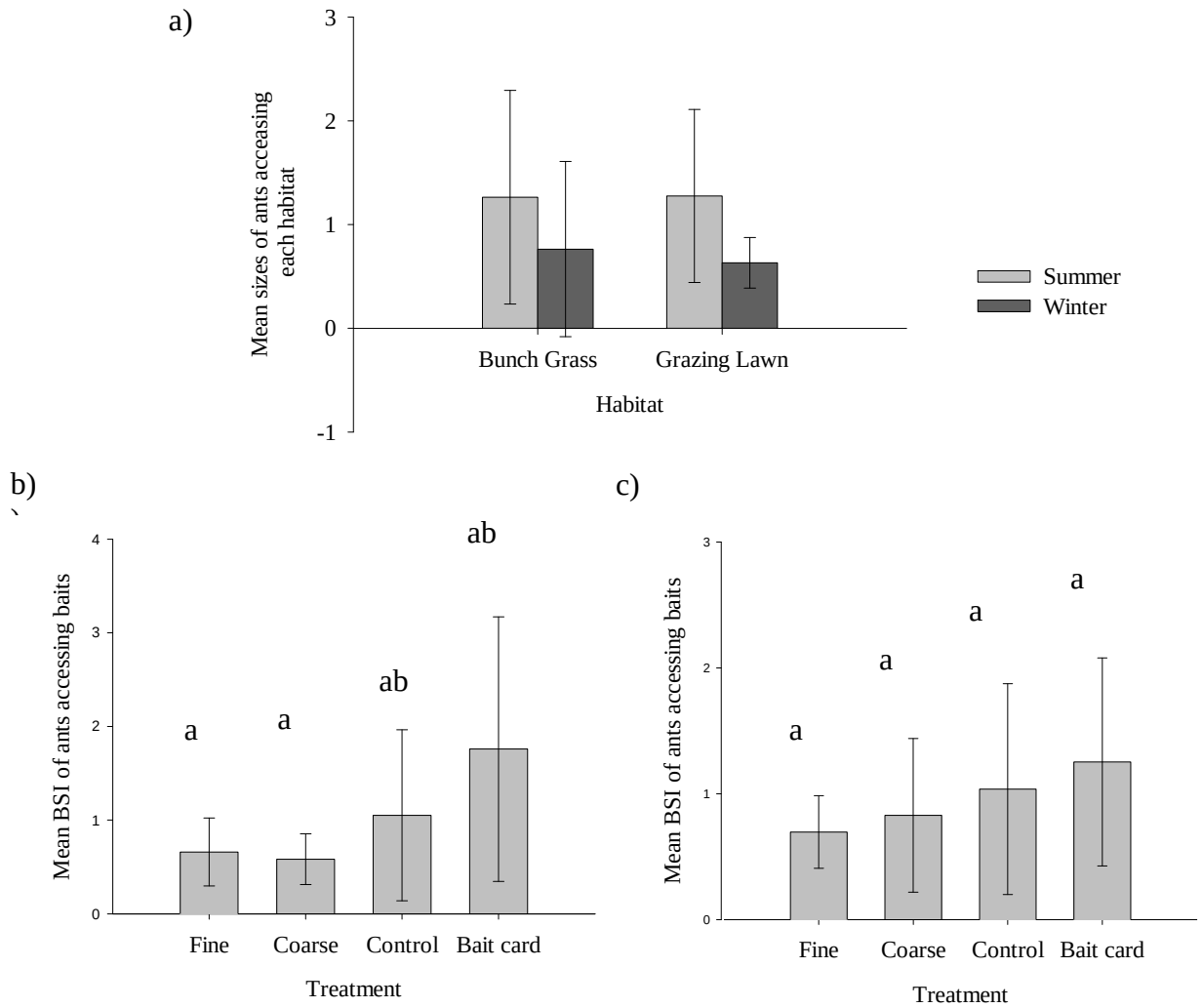


Figure 3.6. Mean (SE) BSI (Body Size Index) ants in the summer and winter seasons in a) the natural complex (bunch grass) and the natural simple (grazing lawn) habitats and b) the manipulated treatments. Bars with similar letters indicate that there is no significance present.

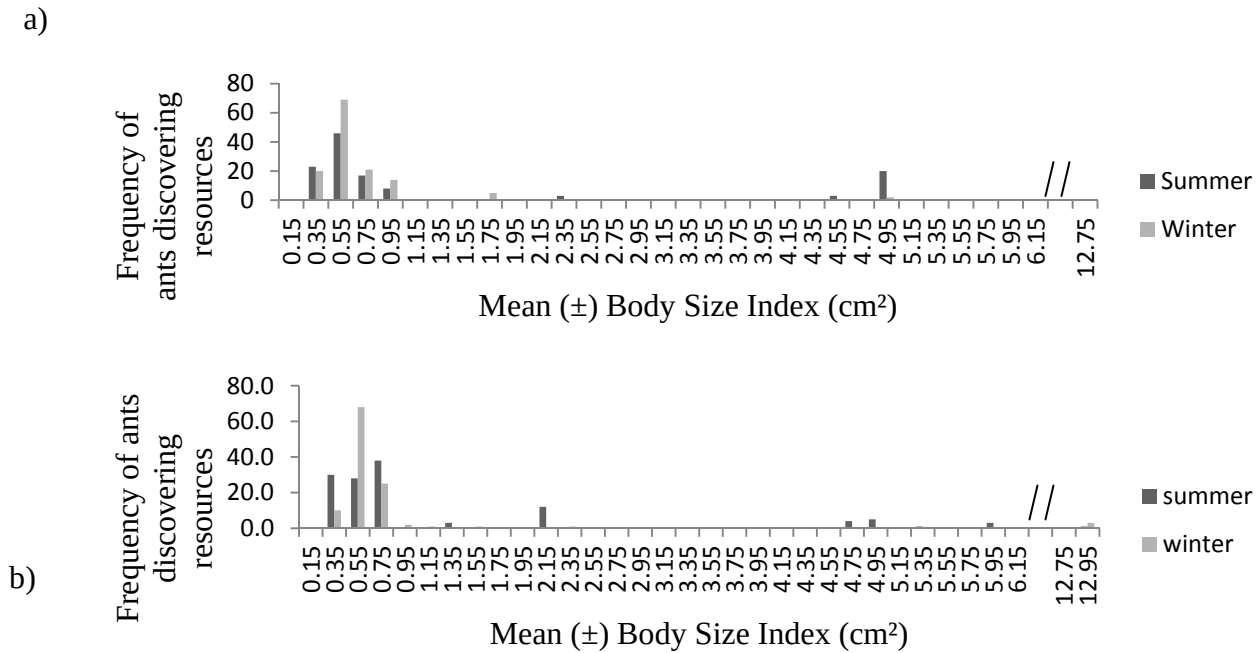


Figure 3.7. Frequency of ants discovering resources within the summer and winter seasons, comparing the BSI (BSI cm^2 = head width x total hind leg length) between the a) structurally complex bunch grass habitat and the b) structurally simple grazing lawn habitat. // indicates a break in the data sequence.

Discussion

Grazing produced two distinctly different habitats. Although the bunch grass habitat and grazing lawn habitat were both dominated by a grass layer they were very different in terms of structural complexity and vegetation composition. This had knock-on effects in terms of the ant assemblage structure and their behaviour. This discussion aims to interpret the findings of this investigation with regard to the natural experiments, manipulated experiments and seasonal experiments.

NATURAL EXPERIMENT

In previous studies disturbances such as grazing have been shown to increase both plant and invertebrate (Gibson *et al.*, 1992; Seymour & Dean, 1999; Read & Andersen, 2000; Joern, 2005) species richness. In this study, this was not the case, as both plant and ant species richness were lower in the grazing lawn habitat than in the bunch grass habitat. However, the

assemblages of the ant and plant communities were significantly different between the bunch grass habitat and the grazing lawn habitat. Results such as these imply that grazing lawns support unique assemblages.

Grazing also aids in the simplification of the ground layer structure which results in behavioural changes from the ants (Sarty *et al.*, 2006). This is because in more open, simpler structured habitats ants are better able to locate and capture food resources (Pik *et al.*, 2001; Lassau & Hochuli, 2004; Gibb & Parr, 2010). Previous studies have shown how habitat complexity influences faunal movement, resulting in significant behavioural changes (Hurlbert, 2004; Tews *et al.*, 2004; Almany, 2004; Lassau & Hochuli, 2005; Lassau *et al.*, 2005;). One such study conducted by Colgan (1989) found that predatory techniques changed with increasing complexity. Sarty *et al.*, (2006) also found that, as habitat complexity increased, the dominant yellow crazy ants' (*Anoplolepis gracilipes*) activities became restricted allowing indigenous, more submissive ants access to resources. Following simplification of the savanna due to disturbances such as fire, ants have been shown to remove higher quantities of seeds and at further distances away from their nests (Parr *et al.*, 2004). The simple ground layer of vegetation enables the ants to traverse the surface rather than climb through, round and over ground cover. Energetic costs of movement are consequently reduced in more simplified environments and this should allow for increased abundance and faster retrieval of resources (Lassau & Hochuli, 2004; Sarty *et al.*, 2006; Nakamura, 2008; Gibb & Parr, 2010). This study did show that there was a higher abundance of ants which appeared to discover resources at a much faster rate in the structurally simple grazing lawn compared to the structurally complex bunch grass habitat. Habitat structure thus acts as a filter affecting resource location and retrieval.

Habitat structure, however, did not appear to affect the dominance-discovery trade-off theory. It is not apparent in either of the two natural habitats as those ants locating resources also tend to dominate them. It was thought that a structurally complex habitat would allow more of the submissive ants access to resources, restricting the more dominant species to the open planar environment (Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007). This study indicated that this was not the case, contrary to the widely held view that habitat structure would affect this trade-off.

MANIPULATED EXPERIMENT

In more planar environments ants are expected to locate and retrieve resources at a faster more efficient rate than in complex environments (Nakamura, 2008; Gibb & Parr, 2010). This

is because structurally complex environments require the ants to travel further through and over and round the vegetation, resulting in high energy costs and longer travel time for similar distances. Secondly, in structurally complex environments, temperatures are reduced due a reduction of radiation penetration, which lowers the ants' activity. Finally, their ability to follow and locate the chemical cues left by other ants is often restricted by complex vegetation structure (Lassau & Hochuli, 2004; Lassau *et al.*, 2005). This study provides evidence to support this pattern as ants located resources faster in the more simple treatments (bait cards and control). However, there was no difference in the number of baits monopolised . This could be related to scale, because the natural experiments as mentioned above indicated that simple habitat supported higher numbers of ants at resources than the complex habitat. Overall, dominance is promoted in more simple environments.

This study also found support for the size-grain hypothesis with the manipulated treatments. This was not the case in the natural habitats as BSI did not vary between them. The SGH appears to be affected by the scale of the study and only at micro-habitat level does it appear to be more important. Habitat structural complexity acts as a filter for body size, therefore restricting certain species of a particular size class (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006; Nakamura, 2008; Gibb & Parr, 2010).

SEASON

Even though ants are able to exist in areas with high temperatures, because of their small body size they are prone to desiccation (Kaspari, 1993). As the experiment only started at 08h00, temperatures at the end of the experiment were extremely high, as is common in summer. These high temperatures probably prohibited the ants, especially the smaller ones, from foraging for resources as the risk of desiccation was too high (Kaspari, 1993). This could explain the presence of larger ants during the summer season and the lack of monopolisation within the natural treatments.

Conclusion

Habitat structure is important to consider as it affects ant assemblages which are important in ecosystem functioning (Folgrait, 1998; James, 2004). Habitat structure within the savanna biome is varied due to disturbances such as grazing and fire (Krook *et al.*, 2007; Mgobozi, 2008). Grazing herbivores are therefore important for the maintenance of heterogeneous areas, by creating grazing lawns (McNaughton, 1979; McNaughton, 1985; Painter & Belsky,

1993; Cromsigt, 2006). The mosaic of grazing lawns and bunch grass areas are desirable for the preservation of diverse ant assemblages. In essence the heterogeneity produced by these mosaics facilitates species co-existence.

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CHAPTER 4

Summary

Several studies have indicated that ants are useful as biological indicators in terms of monitoring disturbances (Andersen, 1995; Folgrait, 1998; James, 2004; Sanders & Planter, 2007). Although they may not reflect the true biodiversity of the area they do represent certain biodiversity losses (Parr *et al.*, 2002). In this study the monitoring of ant assemblages, competitive interactions and biodiversity revealed some mixed results in respect to disturbance. Disturbance typically alters habitat structural complexity (Watling & Norse, 1998), which is also thought to play an important role in the formation of its faunal assemblages, patterns, interactions and biodiversity (Lassau & Hochuli, 2005; Lassau *et al.*, 2005, Gibb & Parr, 2010). This study related ant assemblages, patterns and interactions to the change in habitat structural complexity, which was caused by disturbances. It was found that only certain types of disturbances initiated responses from the ants. Two types of disturbances were investigated, that of an alien invasive plant *Chromolaena odorata* in the Hluhluwe section of HiP and grazing by large mammalian ungulates in the iMfolozi section of HiP.

Grazing by large ungulates results in a compositional change from tall bunch grass species to stoloniferous grazing lawn grass species (McNaughton, 1985; Archibald *et al.*, 2005; Cromsigt, 2006). While the other disturbance that was investigated, the invasive weed *C. odorata*, when it infests the natural bush it results in an impenetrable area that is highly prone to fires (Macdonald, 1983). In terms of management strategies and decisions it is important to know what affect these disturbances will have on the ecosystem. Both these disturbances (grazing by large ungulates and the invasive plant *C. odorata*) exhibited structural changes to a certain degree within the vegetation. When an area became invaded by *C. odorata* structural complexity rose, while a bunch grass habitat that was grazed by large ungulates became less structurally complex. However, only when the bunch grass and grazing lawn habitats were compared was the structure different at ground level. When the infested habitat was compared to an area without *C. odorata* there appeared to be no significant difference between the two at ground level. Similar results were produced when vegetation species composition was compared. Again there was a distinct difference between the grazing lawn and bunch grass habitats, but no compositional difference between the infested and uninvaded habitats. There could be a number of reasons for the similarity in

vegetation composition and structure at ground level. As was mentioned in an earlier chapter *C. odorata* is allopathic, therefore restricting plant growth on the ground level. However, once above ground level *C. odorata* increases in structural complexity, which could restrict the presence of the larger browsing and grazing ungulates. These animals would be unable to access the certain preferable forbs grasses and trees, which are able to grow in amongst the invasive plant. This could therefore be a reason as to why plant composition could remain similar in both habitats. Another such reason could be due to the presence of a large fire that swept through three out of the six control habitat sites before the Braun Blanquet survey, affecting plant composition. These results appeared to have significant effects on the ant assemblages, patterns and interactions within the associated habitats, which is what this thesis addressed.

A set of manipulated and natural experiments (as described in earlier chapters) was set up in both Hluhluwe and iMfolozi to determine the effect of habitat structural complexity on ant interactions and patterns. Conclusions drawn from the iMfolozi experiment reveal that grazing does have a significant effect on ants. This was proven in both the natural and experimental treatments. Season also played a role, influencing the ants behaviour and patterns. Although grazing lawns have often been called overgrazed in the past (Mgobozi, 2008), this study indicates that this may not be the case. There appears to be unique assemblages of both plants and ant species in the bunch grass habitat and the grazing lawn habitat. This is indication enough that the grazing lawn habitat is stable, not overgrazed and able to support unique assemblages of plants and ants. On the other hand results obtained from the natural and manipulated treatments within the Hluhluwe habitats were not as conclusive as those from the iMfolozi habitats. It appears to be a more complex system and only if other factors are controlled for, such as the manipulated experiments will expected results be produced. However, this may all be a result of the fire that occurred within the three control sites, and the fact that structural complexity at ground level remained insignificantly different between the infested and control sites. Structural complexity may be important in this experiment as all the baits were placed at ground level requiring the ants to travel along the surface to access resources. The results from these experiments may provide added information that may help in the maintenance and preservation of biodiversity.

With the conservation of biodiversity in HiP being a priority (Mgobozi, 2008) it is important to know what effects these disturbances will have in order to make accurate management decisions. This thesis aimed to look at the composition and biodiversity of ant assemblages and competition for resources in relation to habitat structure modification by

disturbances. The results were then related to management decisions. The first that was looked at was that of species richness in relation to habitat structure. Species richness is important as ants are typically thought of as reliable biological indicators (Andersen, 1995; Folgrait, 1998; James, 2004; Sanders & Planter, 2007). Ants appear to be positively related to structural complexity, as species richness was higher in the more structurally complex bunch grass habitat and infested habitat. Therefore the use of assemblages, competitive interactions and species behaviour may be used to more accurately to describe the affects of disturbance on the ecosystem.

Secondly this thesis looked at the effect of habitat structural complexity on assemblage composition of ants between the disturbed areas and the intact areas. When looking at the habitats infested with *C. odorata* and those that were not, there appeared to be no difference in assemblage composition. This could be related to the fact that there is no difference between the vegetation communities and structural complexity between the two habitats. Within the grazing lawn and bunch grass habitat there was a distinct delineation of the vegetation communities and structural complexity between the two. The different ant assemblages occurring in the two habitats very closely mirrored the vegetation and structural differences. The assemblage difference within the iMfolozi region between the bunch grass habitat and the grazing lawn habitat suggests to managers that both these are important for the heterogeneity and consequently the biodiversity of the savanna ecosystem (Krook *et al.*, 2007). Therefore the maintenance and preservation of both these systems is a priority. However, results obtained from the infested habitat are inconclusive. Although plant species richness is lower within the infested sites, the ants do not seem to respond positively but rely more so on habitat structure. It may be wise in this instance to use indicators such as spiders as this has been proven to be a valid method in determining the biodiversity loss of invasive plants (Mgobozi *et al.*, 2008). It appears that there are other factors influencing the ants behaviour besides vegetation structure and composition within the Hluhluwe area. This is because when factors (i.e. the manipulated experiment) were controlled for similar results to those obtained from the grazing lawn were produced.

Finally this thesis looked at the effect of habitat structural complexity in relation to competitive interactions using manipulated and natural experiments. In relation to these, four factors were looked at, the first and second being that of the rate of resource acquisition and the number of ants accessing resources. Overall the ants appeared to be highly sensitive to temperature, with intense heat in the summer reducing ant numbers at resources and reducing the amount of time until resource discovery in the grazing lawn and bunch grass habitats.

Hluhluwe appeared to remain cooler in the summer months than iMfolozi. Therefore, the number of ants at the baits rose in summer within the infested and control sites. In the manipulated experiments ants were faster and more abundant in the structurally simple treatments. These results were the same as the natural experiments results in regards to the grazing disturbance. However, the natural experiment in Hluhluwe indicated that there was no difference between the infested and control habitats, again suggesting the complexity of this environment.

The third factor that was looked at was the discovery dominance theory, which suggests that there is a certain trade off between those ants discovering resources and those dominating them (Fellers, 1987; Davidson, 1998; Holway, 1999; Sarty *et al.*, 2006; Adler *et al.*, 2007; Lebrun & Feener, 2007). It was thought that disturbances, which result in habitat structure modification, might alter this relationship between the ants (Sarty *et al.*, 2006). However there appeared to be no such trade-off present in either the control or infested site. This is contradictory to what occurred within the grazing lawn and bunch grass habitats. There was a significant difference in ant assemblages between those discovering resources and those dominating them in both the grazing lawn habitat and bunch grass habitat together and separately. It appears that disturbances such as these do not affect this trade-off but other unknown factors, which need to be, identified in future studies.

Other unknown factors appeared to influence the final factor looked at which was the BSI (body size index) of the ants inhabiting each habitat. It was expected that in more complex environments the BSI of the ants would be smaller than those occurring in the less complex environments (Kaspari & Weiser, 1999; Parr *et al.*, 2003; Farji-Brener, 2004; Sarty *et al.*, 2006). However this was not the case when testing the size-grain hypothesis in the natural treatments, as in the more complex infested site ant species were recorded to have higher BSI's than those in the less complex control habitat. Again this could be attributed to the lack of structural complexity on the ground level, but it is still not clear as further studies on this subject need to be conducted. The BSI of the ants in the natural treatments occurring in the grazing lawn and bunch grass habitats showed no differences, although structural complexity was significant at the ground level. However when other factors were control for in the manipulated experiments the BSI of ants appeared to follow predictions. The simple treatments supported ants with higher BSI than those occurring in the more complex treatments. There also appeared to be a certain threshold required in terms of structural complexity before a change in BSI occurred. This complies with previous studies (Kelaher, 2003) and maybe a reason as to why in the natural experiments the results obtained were

what they are. Season appeared to play the biggest role in the BSI of ants, with the summer months supporting those with larger BSIs than the winter months, as they are less prone to desiccation than smaller ants (Kaspari, 1993).

Structural habitat complexity appears to affect interactions, behaviour and assemblages of ants, especially if other factors are controlled for. Managers should factor this into their decision making process, as disturbances such as grazing add heterogeneity to the area, increasing biodiversity. Other disturbances such as that of *C. odorata* appear to be very poorly understood, in terms of reactions by their associated fauna and flora. It is important to understand the process that governs species interactions within their ecosystems for the maintenance of biodiversity and understanding for future disturbances and habitat modification processes. For example global warming may change the whole dynamic in regards to ant behaviour, interactions and assemblages. As was shown earlier, they are thermophilic, therefore any increase or decrease in temperature will have a significant effect on them. This in turn may have cascading effects within the trophic food web system altering the energy flow through the system. Global warming will also increase the range of *C. odorata* enabling its spread into areas where it did not previously exist (Zachariades & Goodall, 2002). Consequently reiterating the fact that much more needs to be done to determine the effects of *C. odorata* within the ecosystem.

This study adds much needed knowledge of ants, their species, interactions and assemblages within southern Africa to the acquired knowledge already obtained. It also improves knowledge on the importance of disturbances such as grazing and the formation of grazing lawns within the savanna ecosystem. However, it also emphasises how little is known about ecosystem dynamics and interactions, especially in regards to invasion biology

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