Long-term impacts of *Chromolaena odorata* (L.) invasion and ungulate grazing on ant body size and communities in Hluhluwe-iMfolozi Park, South Africa

by

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DECLARATION

I, Nolubabalo Tantsi.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 previously been submitted by me for a degree at this or any other tertiary institution.

Signature :

Date : August 2012

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ABSTRACT

The present study investigated the impacts of Triffid weed *Chromolaena odorata* infestation and ungulate grazing on native ant communities in Hluhluwe-iMfolozi Park (HiP), in KwaZulu-Natal province, South Africa. HiP is a highly valued park because of its unique biodiversity. However, management of biodiversity in this park is intimidated by restructuring disturbances produced by invasions by alien plants and grazing.

C. odorata is a highly invasive plant known to invade to an impenetrable extent, out shading and eliminating all competition of indigenous vegetation to many parts of the world. The rapid invasion and spread of *C. odorata* in natural environments, including large parts of HiP, is making ecosystems unstable as indigenous species decline, thereby resulting in hampered delivering of ecological services. The re-vegetation of *C. odorata* even after control measures has heightened, raises concerns regarding sustainability of indigenous species.

The increase in populations of herbivores in HiP is of concern as vegetation is restructured resulting in interruptions in flora and fauna relations. To increase the understanding of changes associated with these habitat altering disturbances, the effects of invasions by *C. odorata* and herbivory on indigenous communities were investigated.

Ants play diverse roles in terrestrial ecosystems and influence composition, distribution and abundance of other species. Ants are sensitive to changes that influence food abundance, shelter and microclimate. Ants are also strongly linked to a variety of vegetation. Therefore, disturbances that result in displacement of indigenous flora impede the diversity and abundance of indigenous ant species.

Grazing had no effects on ant species diversity but combination of reserve and grass had a significant influence, while rainfall influenced ant abundance. The presence of high rainfall promoted high ant diversity and evenness indicating increased foraging and nesting resources for a variety of ant species. Ant diversity and evenness in areas of high precipitation could also have been caused by moist soils that encourage vegetation growth and cover.

Ant abundance was significantly affected by the combination of reserve, grazing and grass type. High ant abundance was associated with high rainfall, light grazing, and greater vegetation biomass. High ant abundance in lightly grazed exclosures contributed to high vegetation diversity. The lack of ants specializing in lawn grass suggests that this habitat does not contain unique ant communities. However, greater ant diversity found in these habitats, compared to tall grass, confirms that lawn grass provides optional foraging areas and is important for management of ants. This study concludes that rainfall or altitude variations influence ant composition through changes in vegetation growth and diversity more than herbivory.

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CHAPTER 1

General introduction

A healthy ecosystem represents essential resources such as food, clean air, clean water, medicine, clothing and construction materials, which we depend on economically and socially (Gaston 1996; Pullin 2002). For ecosystems to continue to provide these services, the presence of a wide range of species communities is necessary for facilitation and stabilization of ecosystem processes (Callaway *et al*. 2000).

At present, the ecological integrity of many systems is at huge risk due to anthropogenic introductions of invasive alien species and habitat transformation caused by climate change, grazing or anthropogenic fires. Such disturbances result in decreased species diversity and subsequent decline in ecological function and resilience (Tilman *et al*. 1997; Evans *et al*. 2001). Therefore, these habitat-changing disturbances should be assessed and put under manageable levels to reduce their negative impacts on the productivity of ecosystems.

Invasive alien species are introduced species that are non-native, and that have adverse effects on the area that they are introduced into (Richardson & van Wilgen 2004; Raghubanshi *et al*. 2005; Traveset & Richardson 2006). These species may be introduced to new areas by humans either deliberately or by accident and often out-compete indigenous species. For example, French & Major (2001), Wise *et al.* (2007), Sean *et al*. (2008) and Gerber *et al*. (2008) all noted that in other parts of Africa invasive plants completely excluded some indigenous species. This was clearly demonstrated in fynbos areas infested by alien *Acacia saligna*, where ant species such as *Ocymyrmex barbiger* and *Tetramonum oculatum* were noticed to be absent (French & Major 2001). Invasive aliens often modify important aspects of the indigenous ecosystems, such as nutrient formation, hydrology, and plant and animal community structure and composition (Higgins *et al*. 1999; Zachariades & Goodall 2002). Therefore, their presence often negatively affects native species through resource restructuring, competition and alterations of ecosystem processes. Consequently, alien invasive species are listed as the second major threat to maintenance of biodiversity (Jackson *et al*. 2002; Obrist *et al*. 2004). Increased trade among previously segregated continents has been documented as one of the main causes for the alarming increase of biological invasions globally (Williamson 1999; Struhsaker *et al*. 2005).

Invasive alien plants frequently target areas that are disturbed by humans or grazers (Suarez *et al*. 1998; Pysek *et al*. 2002), high nutrient areas and areas with a slow recovery of depleted populations of indigenous plants (Rejmánek 1989; Hobbs & Huenneke 1992). Tropical areas are more susceptible to most plant invasions than acute xeric habitats due to suitable wet conditions that allow growth of seedlings. However, it should be noted that not all invasive alien plants establish in the new host environment. The success of the invasion of an area depends on the compatibility in climatic conditions and environment in the new area and on invasive species characteristics in relation to properties of the invaded ecosystem (Rejmánek 2000).

This study focus on effects of invasion of the shrub *Chromolaena odorata* and ungulate grazing on ant communities in Hluhluwe-iMfolozi Park (HiP) in South Africa.

Alien invasions by *Chromolaena odorata* in South Africa

Problems related to invasive alien species have occurred in South Africa for hundreds of years and can be found in almost all biomes. Approximately 180 invasive alien plants have colonized about 10 million hectares (ha) of South African landscape. The largest part of these invasions come from trees and herbs such as wattles *Acacia meamsii*, blue jacaranda *Jacaranda mimosifolia*, brambles *Rubus* spp., lantana *Lantana camara*, eucalyptus *Eucalyptus camaldulensis* and climbers such as *C. odorata*. The heavily invaded area extends from the Western Cape province, alongside the eastern coastline to the eastern interior (Richardson & van Wilgen 2004). However, the savanna is the most severely invaded of the biomes with the majority of invasions occurring alongside riverbanks (Richardson *et al*. 1997; Rouget *et al*. 2003). One of the most problematic alien plants invading savanna systems is *Chromolaena odorata*.

Chromolaena odorata is synonymously known as Siam weed in English (Muniappan & Bamba 2000), Christmas Bush in West Indies (Chessman 1940), French weed in Laos, Communist weed in West Africa (Laos) or triffid bush in South Africa. It is a foreign aggressive plant belonging to the subfamily Euparotiorieae in the family Asteraceae (Blackmore 1998). The Eupatorium clade comprises about 165 species of the genus *Chromolaena* with species such as *C. ivaefolia* and *C. laevigata* invading areas in North and South Americas while *C. odorata* invades east, west and southern Africa and Asia

(McFadyen 1989). *C. odorata* originates from America and West Indies (Henderson 2001) but has different ecotypes present throughout the world (Bremer 1994). *C. odorata* occurs in two distinct forms that differ in distribution, structure and ecology. The form that invades southern Africa has bright yellow green leaves when young and glabrous fragile stems. It produces white flowers and leaves that produce a sharp odour when smashed. It has rounded furry and nearly smooth shoots.

Chromolaena odorata is a fast growing herbaceous bush with straight fragile stems that are highly branched. It bears three-veined, ovate-triangular leaves with sharp tooth-like edgings (Henderson 2001). *C. odorata* can grow to a height of 3 m in open areas but can reach 10 m as a rambler. The *C. odorata* plant reproduces sexually when it is a year old resulting in substantial number of seeds (Witkowski 2000). Small, light seeds of 0.2 mg and 5 mm in length are produced (Henderson 2001). Seed germination is triggered by the presence of water and light, and occurs during the wet season (Muniappan & Bamba 2000). When unfavorable conditions prevail, seeds remain dormant in the soil but re-germinate when conditions become favourable. In South Africa, *C. odorata* produces massive amounts of seeds until the age of 10 years after which the seed production reduces (Witkowski & Wilson 2001). The rapid spread of *C. odorata* relies on wind or attachment to animal fur.

Chromolaena odorata invades tropical and subtropical areas where there is no frost. In Africa, the arrival of *C. odorata* was first observed in Nigeria around 1937 and was further identified as a pest in cocoa farms where it escaped colonizing surrounding countries such as Ghana, central, western and eastern parts of Africa in 1960's, but the form was the Asian-Western ecotype (Adenikinju 1975; Obatolu & Agboola 1993). The ecotype of *C. odorata* that infests South Africa is from the Caribbeans. It has bright yellow green leaves when young and glabrous fragile stems. It produces white flowers and leaves that produce a sharp odour when crushed. It has rounded furry and nearly smooth shoots. It settles in all soil and vegetation types such as woodland, grasslands and arid bushveld. It occurs in elevated areas of up to 1500 m above sea level (Blackmore 1998) and targets newly disturbed areas and can grow successfully in areas receiving rainfall from less than 500 mm per year to above 1500 mm annually (McFadyen 1991). The historical traces of the first arrival of *C. odorata* in South Africa are uncertain. Some studies reveal that *C. odorata* first arrived in South Africa in Cape Botanical Gardens around 1850 in mid-eighteenth century (Hilliard 1977) while Liggitt (1983); Erasmus (1988) and Zachariades *et al*. (2004) confirm that this biotype first arrived in South

Africa, to the Durban harbour, KwaZulu-Natal, in the 1940's. *C. odorata* spread rapidly and it infested surrounding areas through enormous seed production and dispersal (Robertson *et al*. 2003).

The presence of *C. odorata* in native systems can reduce establishment of native flora and affect water quantity and quality (Sajise *et al*. 1974; Goodall & Erasmus 1996; Zachariades & Goodall 2002). For instance, in Thailand *C. odorata* reduced pollination by butterflies by attracting them more than indigenous trees (Ghazoul 2004). In South Africa, invasions of *C. odorata* has been suggested as a cause for reductions in population sizes of black rhinoceros *Diceros bicornis* and crocodiles (*Crocodylus niloticus*) in St Lucia (Leslie & Spotila 2001; Reid *et al*. 2007), and to negatively affect diversity and abundance of spider communities (Mgobozi *et al*. 2008), mammals (Dumalisile 2008) and ants (Julius 2007) in HiP.

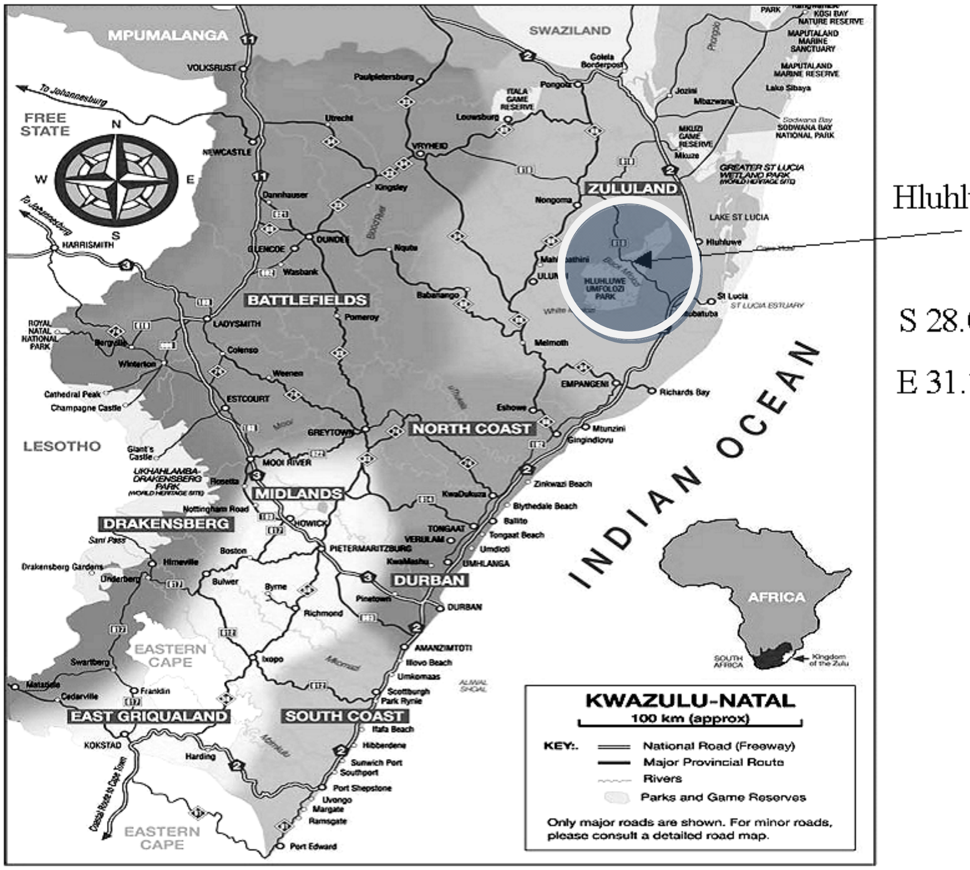
Efforts to prevent the spread of *C. odorata* include physical removal in conjunction with chemicals and natural predators. In South Africa, some areas are cleaned by hand pulling and use of herbicides. This is done with the assistance from governmental (Working for Water) and non-governmental organizations such as the *Chromolaena* Clearing Programme (MacDonald 1983). These measures have proven successful in restoring native biota and decreasing *C. odorata* to manageable levels, but these measures are expensive and therefore are not always easy to deploy. The use of biological controls is therefore preferred. Agents such as the leaf-eating moth *Pareuchaetes insulate* and the seed eating weevil *Apion brunneonigrum* have been confirmed to retard *C. odorata* germination in many countries (Cruttwell 1972). Unfortunately, in South Africa, biological control seems ineffective to decrease *C. odorata* infestation to manageable levels due to weather conditions that are unfavourable for most biological control agents to thrive (Zachariades & Strathie 2006; Zachariades *et al*. 2009). For long-term management of *C. odorata*, removal of *C. odorata* and re-cultivation of resident vegetation and the use of all control measures including fire at greater intensities, are recommended (Luwum 2002; Marais 2004; Van Gils *et al*. 2004; tee Beest 2010).

Study area

HiP is one of the oldest protected areas in Africa. It was proclaimed in 1895 and occupies the foothills of the escarpment to the west of the coastal plain of northern KwaZulu-Natal province, South Africa (Fig 1.1). The park covers an area of about 96,000 ha and is formed by the amalgamation of two sections; iMfolozi and Hluhluwe. The more arid and much larger iMfolozi section occupies about 66,000 ha and is located in the southern part of the Park while Hluhluwe is more mesic occupying about 30,000 ha of the northern parts of HiP. Mean daily temperatures and precipitation vary with months but are both strongly correlated with elevations. The wet and warm summer season experiences temperatures ranging between 14 °C and 40° C, while in winter temperatures range between 6° C and 34° C (Zululand Tree Project baseline data). Rainfall is seasonal and occurs mostly in spring and summer within the months of October and March. The northern Hluhluwe region receives precipitation of approximately 985 mm per year compared to the southern and low-lying western regions that receives an average of approximately 700 mm.

Hluhluwe-iMfolozi Park is found within the savanna biome and consists mainly of the lowveld class of the tropical bush savanna and Zululand thornveld (Acocks 1988). HiP contains a wide range of plant and animal life. Over 1200 plant species occur in the park and vegetation types include savannas, grasslands and thick shrubs. Plant genera in the savanna include the shrubs *Dichrostachys cinerea*, *Euclea and Acacia*, as well as grass species of *Themeda trianda*, *Urochloa mossambicensis*, *Digitaria longiflora and Dactyloctenium australe.* Trees such as Marula *Sclerocarya birrea* and *Acacia burkei* are also common in savanna areas. *Acacia karroo, Acacianilotica Acacia nigrescens*, *Acacia tortilis*, *Acacia burkeii*, *Schotia brachypetala*, *Spirostachys africana* and *Sclerocaryabirrea subsp. Acarcia caffra* constitute common vegetation (Conway *et al*. 2001). In the Hluhluwe region, the dominant vegetation is the wild palm *Harpephyllum cuffrum* and white stinkwood *Celtis Africana* while *Acacia tortilis* and *Acacia nigrescens* replace these two species in iMfolozi.

The dominant grazers in the park include plain zebra *Equus quagaa*, impala *Aepyceros melampus*, white rhinoceros *Ceratothemium simum*, warthog *Phacochoerus africanus*, buffalo *Syncerus caffer* and blue wildebeest *Connochaetes taurinus* whereas the elephant *Loxodonta africana,* greater kudu *Tragelafus strepsicores,* nyala *Tragelafus angasii*, giraffe *Giraffa camelopardalis* and black rhinoceros *Diceros bicornis* constitute the dominant browsers (Whateley & Porter 1983). Currently, impala are the most abundant herbivores in the HiP followed by white rhinoceros (Carla *et al.* 2009). However, the quantity of species in the Park has changed over the years due to habitat transformations caused by diseases, fire, grazing and invasive aliens. HiP has been infested by *C. odorata* since 1960 (Macdonald 1983). In 2001, *C. odorata* was reported to have invaded about 5 600 ha within HiP threatening indigenous flora and fauna (Howison & Balfour 2002) (See Map Fig 1.2). At HiP, South Africa, it infests mostly savanna systems that have much drier climatic conditions than its place of origin (Howison 2009).



Hluhluwe iMfolozi Park

S 28.0000-28.4300

E 31.7160-32.0150

Fig 1.1: Map showing study place Hluhluwe-iMfolozi Park in South Africa (Waldram 2005).

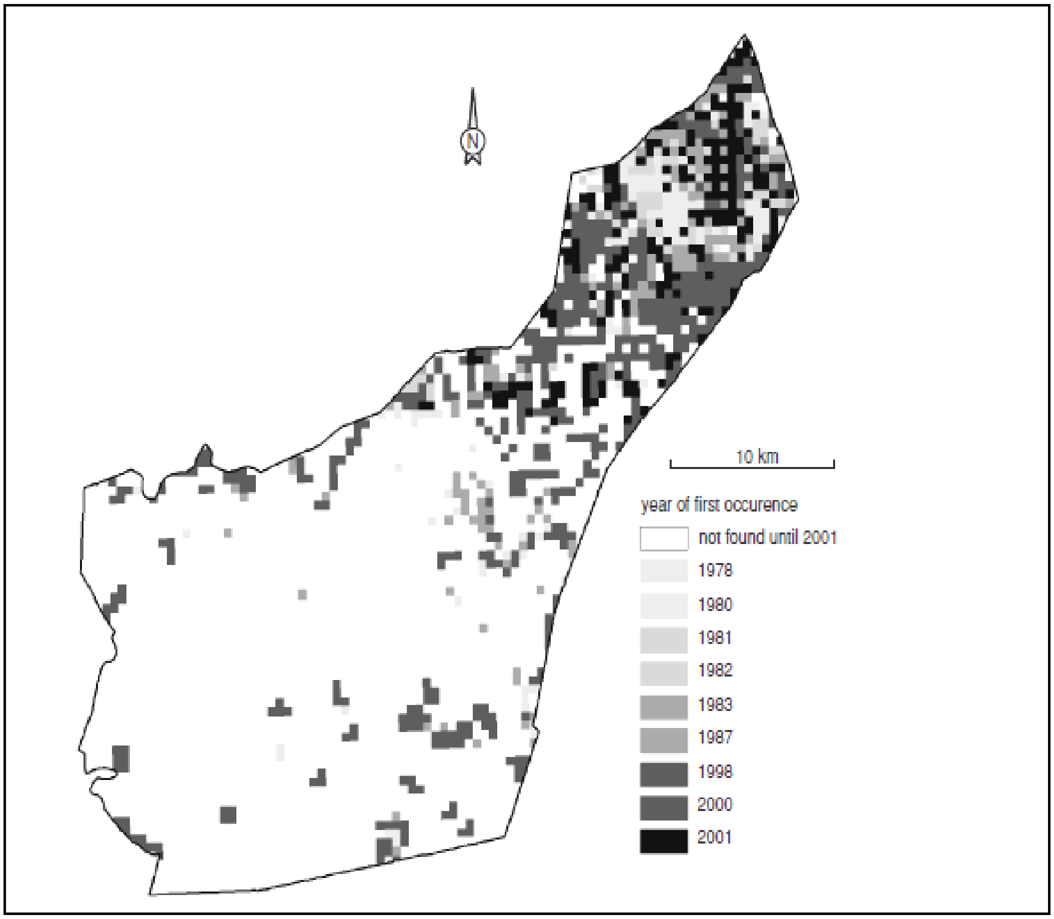


Fig 1.2: Map showing *Chromolaena odorata* spread and distribution since 1970's to 2001 in HiP. The northern part (Hluhluwe) has been most severely infested (Howison 2009).

Grazing in African savannas

Savanna ecosystems occur widely throughout Africa and are mostly composed of woody vegetation and grasses (Cole 1986). Savannas contain heterogeneous flora that present diverse habitat and food resources and allowing co-occurrence of different grazers. According to early research, utilization of specific vegetation components by certain grazers evolved as a result of competition for floristic resources (Jarman & Sinclair 1979).

Studies on grazing have been conducted by different scientists and findings suggest that grazing has negative effects on biodiversity in savanna ecosystems as they alter soil chemistry, vegetation biomass and stature, thereby affecting species distribution (Bock *et* *al*. 1984; Edge *et al*. 1995). For example, the ant *Rhytidoponera metallica* feeds on senescent vegetation and its population size decreased when old-grown vegetation was cleared by herbivory (Bestelmeyer & Wiens 1996). Another study in Kenya showed a decrease in small mammal populations and diversity with the presence of grazing (Keesing 1998). However, some studies have revealed that grazing benefits some organisms by increasing forage opportunities for herbivores, and increase flora growth and diversity by removing old and dry grasses (McNaughton 1984). Go'mez & Gon'zalez-Megias (2007), however, revealed that variation in species responses to grazing is caused by variations in niche requirements (Curry 1994). For example, some organisms inhabit shaded and complex areas to escape from predators. Such organisms include spider species from the genus *Argiope* that was shown to disappear when exposed to open areas (grazed areas) due to their preference for complex habitats (non-grazed areas), while spiders from the genus *Aelurillus* increased in biomass in exposed areas.

Interactions between herbivores and plants have existed for over millions of years. As a result, plants have adapted to defoliation by herbivores in various ways. For instance, some grasses have adapted to grazing by protecting themselves using a hard lignin cover that makes grazing difficult, while others exude toxic chemicals that decrease their palatability (McNaughton 1984). Grass in continuously grazed areas often adapt to grazing by remaining short in stature. This phenomenon has gained much attention in the literature on savanna ecology (McNaughton 1984; McNaughton & Georgiadis 1986; Augustine & McNaughton 1998) and causes a specific type of open grassland known as grazing lawns (Dennis *et al*. 1998; Kruess & Tscharntke 2002; Bailey & Whitman 2003). Grazing lawns were first recognized in the 1960's in Zambia and Uganda where grazing by hippo (*Hippopotamus amphibious*) created large open patches containing short grasses (Olivier & Laurie 1974). These grasses were previously associated with habitat degradation by early pasture managers and were therefore strongly disapproved of. However, current literature revealed that grazing lawns are common components of savanna systems that result from intense grazing of bunch grass by herbivores, and these and tall grass are the dominant grass in savannas.

Grazing lawns produce unique and nutritious grasses due to eutrophic soil resulting from herbivore excreta (Page & Walker 1978; Thompson-Hobbs 1996; Cromsigt & Olff 2008), unlike tall grasses that take over in areas without or with only moderate defoliation (Coughenour *et al*. 1985). Since the composition of grass communities in grazing lawns are different from other grass communities in savannas, these grasses are suggested to be a stable grassland community that contribute to heterogeneity of species in savannas and are significant in conservation of species (Bond *et al*. 2001). For example, Mgobozi *et al*. (2008), and Krook *et al*. (2007) found special species and higher species diversity, abundance and richness of spiders and bird in lawns than tall grass. However, differences in species richness, diversity and abundance among the grass types in savannas are rarely documented although this information is important for management of species that require habitat heterogeneity.

Ants as indicator species for environmental modifications

The significant increase in the number of environmental disturbances has given rise to a need for further research to quantify the ecological effects of environmental change. Due to complexity of most ecological systems, individual species are often used as bio-indicators of environmental processes. Surveys of such indicator species often help guide land managers and decision makers to identify environmental disturbance and subsequently to take actions in time to reduce damages. The use of invertebrates as indicators for environmental modifications and integrity has an extensive background from aquatic ecosystem monitoring (Cairns & Pratt 1993; Andersen *et al*. 2004). However, in terrestrial ecosystems the use of invertebrates as environmental indicators has only recently gained attention (Gómez, *et al*. 2003). Ants have been identified as good indicators in terrestrial environments because of their high abundance, low sample effort and their immediate responses to ecological changes (Bestelmeyer & Wienes 2001; Andersen *et al*. 2002; Parr *et al*. 2002; Scott & Hochuli 2004). Ants contribute to the continued existence and abundance of other organisms at higher trophic levels (Carroll & Janzen 1973; Andersen 1990; Holldobler & Wilson 1990; Vickery *et al*. 2001). For example, ants are a principal diet of many other animals, including Cape pangolins *Manis temminckii* (Swart *et al*. 1999) and humans in some parts of Africa (Davidson 2006). Ants act as defenders of plants and are generators of soil nutrients (Folgarait 1998; Read & Andersen 2000; Heloise & Dieter 2004), and they occupy a wide variety of environmental niches making it possible to show responses of other invertebrates inhabiting the same niche spaces (Holldobler & Wilson 1990). Ants feed on seeds, leafy parts of plants and some are hunters (Holldobler & Wilson 1990). Their increase in diversity and abundance is also positively correlated to vegetation diversity.

The historical use of ants as indicators of ecological systems started in Australia in the mid 1970s and focused on assessing the environmental impacts of mining (Majer 1983), herbivory (Andersen *et al*. 2004), agricultural intensification and forest disturbances (Neumann 1992; York 1994; 2000). A multitude of previous studies showed that ants do not always show uniform responses to disturbances and this is caused by differences in ecosystems, places where a disturbance occurs, duration of a disturbance in the ecosystem, concentration of a disturbance and differences among ant species (Majer & Beeston 1996; Landsberg *et al*. 1997). Some studies have revealed that fire and grazing benefit ant species abundance and species richness by providing an increased surface area for food and foraging (Andersen 1998). In South Africa, ants have been used to assess ecological responses to mining in arid Namaqualand coast (Netshiphala 2005), exotic plants (Donnelly & Giliomee 1985), fire (Parr *et al*. 2002), pesticide use (Witt & Samways 2004), livestock grazing (Tshighuvo *et al*. 1999) and logging practices (Andersen 1997; King *et al*. 1998). A study on mined habitats (Netshiphala 2005) showed that mining influences the abundance and species richness of ants with more ants in un-mined habitats compared to previously mined habitats undergoing restoration. Another study revealed that increased shading due to increased complexity negatively affected ant distribution because cold microclimates become unsuitable for ants (Scott & Hochuli 2004). Andersen (1997) revealed that ant richness and composition at mine sites undergoing restoration reflected re-establishment by other invertebrate groups, suggesting their usefulness as indicators.

Rationale and Research approach

It is in South Africa's interest to protect our ecological systems and conserve its diversity. However, the continued colonization of savanna systems by foreign species is making conservation of biodiversity difficult. *C. odorata* has spread tremendously in South Africa over the years despite manual and chemical clearing measures taken to manage it. Long-term ecological presence of *C. odorata* raises concern about long-term sustainability of native species and ecosystem properties. In order to understand the response of ant communities to habitat changes related to *C. odorata*, ant populations from *C. odorata* infested areas, non-infested and cleared areas were compared in terms of abundance, species composition and body size. This study compares ant communities in areas that have been infested for different time periods, as well as areas where different time periods had passed since clearing. Furthermore, effects of different grazing levels, and grass type and rainfall on ant communities were examined by comparing ant diversity, number and body size from two sections of HiP with three grazing levels (non-grazed, low grazed and high grazed) and four grass types. The study will help management and policy makers to evaluate the impacts caused by invasive aliens. It can therefore aid in management of aliens and long-term conservation of native species. On grazing, management will obtain a better understanding of the effects caused by ungulate grazing on invertebrates.

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CHAPTER 2

Long-term effects of Triffid weed *Chromolaena odorata* infestation on ant body size and communities in Hluhluwe-iMfolozi Park, South Africa

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Abstract

Over the past decades, the impacts of invasive alien organisms have become a major concern for biodiversity conservation. The Triffid weed, *C. odorata* is a plant that has become invasive in Hluhluwe-iMfolozi Park (HiP) and has been confirmed to completely eliminate all kind of indigenous species and halt ecosystem service delivery. Rehabilitation of *C. odorata* in infested sites through physical, chemical and biological measures is a common practice and has proven successful in preserving indigenous systems. However, studies comparing the short and long-term effects of *C. odorata* invasion and clearing are rare.

Ants play important functions in terrestrial ecosystems, and invasion by alien plants is changing indigenous species composition worldwide. This study focuses on understanding the changes brought by *C. odorata* invasion over a short and long-term on indigenous biodiversity in HiP. This study investigated how ant diversity, abundance and morphological features varied across six areas in HiP that had different levels of *C. odorata* invasion and times since clearing. There were no significant effects of *C. odorata* invasion or clearing on ant diversity and abundance, but there were significant differences between seasons. Ants were more abundant and diverse in spring compared to winter, indicating high heterogeneity in food and habitat resource in spring. The results suggest that *C. odorata* has no effect or limited effects on ant communities, but that there were seasonal variations in ant abundance and community structure.

Introduction

Over the past decades, the impacts of alien invasive organisms in unharmed environments have become a major concern in biodiversity conservation (Lonsdale 1999). The effects of alien invasives have been documented on aboitic processes, biological organisms as well as whole ecosystems (Bamba *et al*. 1993; Wagner 2001; Ambika 2002; Crooks 2002; Mangla *et al*. 2008). They also affect ecosystem services, native species heterogeneity and community composition (Mack *et al*. 2000; Levine *et al*. 2003). However, environmental impacts of invasive alien organisms on are not easy to measure, and require a broad understanding of the functioning and structure of the affected ecosystem (Castley *et al*. 2001).

C. odorata is a troublesome and aggressive perennial shrub that originates from tropical Americas. This plant infests both altered areas such as forest margins and unaltered areas such as roads. It also occupies non-vegetated areas but disappears immediately when indigenous vegetation grows. *C. odorata* negatively affects subsistence farmers by invading land and reducing crop production, decrease pasture quality and native vegetation diversity by outcompeting resident species for resources necessary for effective growth. *C. odorata* has been confirmed to hinder native ecosystem succession through its dense threads (De Foresta & Schwartz 1991) and suppress specific food for some animals (Van der Hoeven & Prins 2009).

In South Africa, unlike its place of origin, *C. odorata* grows mostly in drier areas in the savannas (Goodall & Erasmus 1996). The Hluhluwe-iMfolozi Park (HiP) is an area rich in biodiversity, and is inhabited by herbivores and carnivores such as elephant (*Loxodonta africana*), lion (*Panthera leo*), nyala (*Nyala angasii*), leopard (*Panthera pardus*), buffalo (*Syncerus caffer*), wild dog (*Lycaon pictus*), black rhino (*Diceros bicornis*), and white rhino (*Ceratotherium simum*), and a diverse number of flora species, hence its strong conservation status in South Africa (Brooks & Macdonald 1983). HiP has been colonised by *C. odorata* since the 1960's (Macdonald 1983), and indigenous species are subsequently at risk (Sala *et al*. 2000). The mapping of *C. odorata* in HiP first occurred in 1985 when the north-east section of the reserve had just been infested. Although still at low densities, *C. odorata* infestation in HiP had spread at the end of 1990s, and two decades later, it was confirmed that the invasions could completely devastate the entire park within the next ten years (Macdonald 1983). About 20 % of HiP was estimated to be under intense *C. odorata* infestations in 2001, with infestations being particularly severe in the northern part of the park (Hluhluwe) (Howison 2009). Measures to put *C. odorata* under controllable levels are followed including follow-up efforts which remove re-germinating *C. odorata* seedlings (Van Gills *et al*. 2004). According to Dumalisile (2008), Mgobozi *et al*. (2008) and, Julius (2007), *C. odorata* removal restores the previously degraded ecosystem to close to its original condition. Mgobozi (2008) and

Dumalisile (2008) also confirmed that the earlier the system is freed from invasion, the quicker it will return to its original state before the invasion. However, these findings have only been confirmed on spiders and small mammals, and cannot be generalized for all species living in HiP, hence the assessment of ant response to long and newly *C. odorata* infestation in the current study.

Ants are important components of many terrestrial ecosystems. They have been extensively used to diagnose various ecological modifications and are regarded as reliable indicators for ecosystem disturbance. They are ecologically dominant species that act as seed pollinators, seed-dispersers, food for animals and vegetation protectors from herbivory. They can have strong effects on plant abundance and composition and are quick to respond to habitat transformation (Hughes & Westoby 1992). Therefore, if the presence of aliens such as *C. odorata* has degrading influences on local ant communities, it may have cascading effects on native vegetation and as well as animals that feed on ants. In addition, the thick structural and shaded environment generated by *C. odorata* is an important conservation concern because some organisms such as neotropic ants may abandon cold shaded areas. The current study aspires to investigate the degree of change in native ant communities in patches with varying time periods having elapsed since *C. odorata* infestation or clearing and removal in HiP. This was done by (i) determining if ant species richness, diversity, abundance and distribution vary in relation to *C. odorata* invasions and clearings or removal, (ii) determine if ant body size varies in relation to *C. odorata* invasions and clearings or removal (iii), investigate if seasonal variation has an effect on ant communities. This was done following the hypothesis that seasonal alterations in temperatures will affect food resources and vegetation composition.

Based on studies by Kaspari (1993), Kaspari & Weiser (1999) and Parr *et al*. (2002), the expectation is that smaller body sized ants will dominate in *C. odorata* infested areas because of decreased environmental spaces compared to unaffected areas. These spaces are typically smaller than the indigenous vegetation and may therefore provide for easier foraging for small organisms while it hinders bigger organism efficient movements. According to Parr *et al*. (2002) and Gibb *et al*. (2006), as small ants shift from structurally complex to open areas, the leg length also increases to reduce locomotion costs. Small ants will inhabit complex areas to reduce dehydration risks. Less ant diversity, richness and abundance is expected in infested areas due to monotonous and structurally thick vegetation that reduces light penetration, making the environment unsuitable (Ellison *et al*. 2002).

A long period of disturbance in an environment has far more degrading effects than when a disturbance has occurred for a short period (Strayer *et al*. 2006). Thus, areas infested for a long period are expected to demonstrate more deteriorated conditions with lower ant diversity, richness and abundance compared to newly infested areas. Areas cleared for a longer period of time are hypothesized to have a higher ant abundance and richness than newly restored treatments as these have a longer time to recover.

Materials and methods

Treatments and sampling procedure

Samples were collected during 2005 and 2006 (Mgobozi *et al*. 2008). I sorted and identified the ants. These samples were taken from six different treatments which included a one newly infested area (*ca* 2 years), two areas with old infestations (*ca* 10 year and 20 year), an area that had recently been cleared from *C. odorata* (*cl* 2 year), an area that had been cleared for a longer period (*cl* 5 years), and an area which had not experienced *C. odorata* infestation. Each treatment had six replicate sites which were placed 200 m apart resulting in a total of 36 sample sites. All treatment sites were situated in areas of similar vegetation (dominated by *Celtis africana*) and aspect (Mgobozi *et al*. 2008). The samples were collected in four seasons, that is, in summer, winter, spring and autumn. However, in this study only samples collected in spring and winter were chosen because they contained high numbers of ants. Within each of the treatment sites, ten pitfall traps were positioned in a rectangular grid (2 m x 8 m). This sampling method is regarded to be efficient in presenting information on species composition, diversity and abundance of ants. This is also easy to employ and maintain (Kjar & Barrows 2004). The traps were set 2 m apart from each other. Small plastic cylindrical vials (honey jars, 3.5 cm wide x 13 cm deep) containing a mixture of water/propylene glycol and a small amount of liquid soap were depressed up to their rims into the holes that were dug into the ground with an auger. The traps were left open in the field for three days. This was meant to target individuals foraging at various times as mentioned by Gibb & Hochuli (2002). Ants were separated from other invertebrates in the field and transferred into small closed plastic tubes containing 70% alcohol that were labelled according to treatment, site and trap number. Ants were later identified according to species and measured. All species identifications were verified by comparing the specimens to a reference collection. For random selection of individuals and avoiding bias, a transparent petri-dish with a diameter of 13 cm with the ants suspended in 70% ethanol was laid over a rectangular grid. A table of random numbers was used to randomly select ant specimens in grid squares. Ant specimens were identified by utilizing a Zeiss DV4 32-X dissecting microscope equipped with ocular micrometer which was accurate to 0.01 mm. In addition to being identified to species or morphospecies, ants were also classified into functional groups. Analyses of functional group to disturbances are important for predicting ant responses when species level information is lacking (Anderson 1990).

For body size measurements, 3 to 30 worker ants from species that were available in adequate numbers in infested, cleared and non-infested treatments were selected. Species included in the body size measurements were *Pheidole* sp *A*, *Pheidole* sp *B*, *Pheidole* sp *G* and *M. delagoense*. Linear measures were taken to the nearest 0.1 mm using a measuring slide under a microscope. Parts measured included, (a) maximum head width including eyes (b) maximum head width excluding eyes (c) maximum head length (d) hind tibia length (f) and hind femur length. A body size index was calculated by multiplying total head length (mm) and leg-length (mm). According to (Sarty *et al*. 2006), this index captures the size of an ant as well as its ability to move through environmental spaces.

Data analysis

Ants were identified to species level and the relative abundance of each specimen within each species and treatment recorded. Body size and abundance data were log transformed to evaluate equally dominant and rare species. Two-way analysis of variance (ANOVA) was employed to investigate the effect of *C. odorata* and season on ant composition using statistical package SPSS version 17.0. Three-way analysis of variance was calculated to examine the effect of treatment, season and species on body size index. Post hoc tests were used where significant differences existed. A Paired t-test was furthermore used to investigate species in each season within treatment that obtained smaller or larger body size index. P-values from t-test were further adjusted for multiple comparisons using a false discovery method (Benjamini & Hochberg 1995).

To further examine variations in species composition between the treatments, the software PRIMER version 6 was used. Data transformation by square-root transformation was prepared to reduce the contributions of quantitatively common and noticeable species to the same level as uncommon species. Multivariate statistical analyses, Analysis of Similarity and Bray-Curtis similarity were used to investigate similarities between treatments. A non-metric Multi-dimensional scaling (nMDS) was performed to graphically illustrate differences and similarities in ant assemblage composition between treatments. In non Multi-dimensional scaling, two points occur closely to each other when they are mostly alike and occur distantly when different. Furthermore, differences in ant assemblage structure between treatments were examined using Analysis of Similarity (ANOSIM; R). The test statistic R investigates and quantifies the degree of similarities or differences between treatments, and range from R= 0 indicating no differences between treatments to R = 1 indicating complete dissimilarity. The pairwise test between treatments identified between which treatments differences or similarities existed. Similarity Percentage test (SIMPER) was additionally calculated to determine species that contributed to differences or similarities. In Simper, two treatments constitute a similar complement of species with identical abundances and have different species if their similarity is 0.

Ant communities were also quantified across the six treatments using three diversity indices:

Shannon-Weiner index (H’) was used to estimate species diversity. This index is good at capturing environmental trends because it includes relative abundance of species and penalize unevenness in these abundances:

$$H' = -\sum_{i=1}^{n} p_i (\log_2 p_i)$$

where n denotes number of species and p_i is the proportion of the total count arising from the i’th species (Clarke & Warwick 1994).

Margalef’s index (d) was calculated to estimate species richness (Odum 1971):

$d = (S - 1)/\log N$

where S signifies total number of species; N is total number of individuals.

Simpson’s Index ($1-\lambda$) quantifies the abundance of common species, and was calculated as:

$$1-\lambda = -\sum_{i=1}^{k} p_i^2$$

where k denotes number of species and p_i is the proportion of the total number of ants found in one trap that belong to species i.

Results

Ant diversity, abundance and richness

A total of 16 ant species were recorded (Table 2.1). The most species rich genera in all treatments were *Monomorium, Tetramorium* and *Pheidole* with four species each followed by one species each from *Anoplolepis*, *Myrmica* and *Pletrotera*. Eleven ant species were found in winter while 14 species were found in spring. Unique species found in spring were *Tetramorium* sp *C*, *Tetramorium constancia*, *Tetramorium* sp *G*, *M. natalensis* and *Pletrotera* while two species of *Pheidole* were the only unique species in winter. Freshly cleared areas were highly dominated by one ant species (*A. custodians*). Long cleared habitats inhabited mostly *Tetramorium* sp *C* (27 %) followed by 20.3 % of *Pheidole* sp *A* and *Monomorium* sp *A* (13 %), while a highest percentage of *Anoplolepis custodians* (60.2 %) dominated newly cleared areas. The 20 year old infested treatment contained about 22 % of *Myrmica natalensis* and *Pheidole* sp *A* (23 %), while a 10 year infested area obtained high abundance of *Monomorium delagoense* (23 %) followed by *Pheidole* sp *B* (18 %), 16 % *A. custodians* and *M. natalensis* (14 %). Non-infested habitats had highest numbers of *Pheidole* sp *G* (43 %) and *M. delagoense* (26 %). Species shared in all treatments was *Pheidole* sp *B*.

There was no significant effect of treatments ($F_{5,\,75}$= 1.45, P = 0.22) or season ($F_{1,\,75}$ = 0.007, P = 0.93) on ant abundance and diversity, but there was a significant effect of season on ant species richness ($F_{1,\,150}$ = 19.42, P = 0.000). Spring (9.07 ± 0.51, mean ± SE) obtained higher ant species richness than winter (6.00 ± 0.39). The most abundant species in spring was *Anoplolepis custodians* (28 %), the second *M. delagoense* (20 %) and *M. natalensis* (15 %), while *Pheidole* sp *G* (38 %) *and Pheidole* sp *B* (16 %) dominated in winter. None of the diversity indices showed any significant differences between the treatments (Table 2.2).

The nMDS also illustrated similarities in community composition between treatments (Fig 2.1), although the ANOSIM (Global R = 0.393, *P* = 0.001) showed differences in ant communities between treatments (Table 2.3). The SIMPER analysis indicated that treatments were very similar as most species were shared. Unique species characteristic to treatments included *M. natalensis* in the 20 year infested area, *A. custodians* in the 10 year infested area and *Tetramorium* sp *C* in the long cleared areas. Dominant species that contributed most to the similarities between treatments included *M. delagoense* (48.1 %) and *Pheidole* sp *B* (27.3 %) in 10 year infested habitats while *Pheidole* sp *A* (31 %), *Pheidole* sp *B* (21.5 %) and *M. delagoense* (16.2 %) highly contributed to similarities in a 20 year infested area (Table 2.4). In newly infested areas, the dominant contributors were *Pheidole* sp *G* (87.3 %) and *M. delagoense* (11.04 %) while 2 year cleared compartments had their contribution mostly dominated by *Pheidole* sp *G* (79.9 %), *Pheidole* sp *A* (8.31 %) and *Pheidole* sp *B* (6.78 %). However, *Tetramorium* sp *C* (27.3 %), *Pheidole* sp *A* (27 %) and *Pheidole* sp *B* (13 %) were the dominant contributors in 5 year cleared areas compared to non-infested areas which were mostly contributed by *Pheidole* sp *G* (49.9 %) and (33.86 %) from *M. delagoense.*

Ant body size

There was a significant interaction effect of treatment, season and species on ant body size index ($F_{3,\,302} = 2.77$, $P = 0.042$; Fig 2.2). In general, most species showed an increase in size in both treatments within the spring season except for *M. delagoense* and *Pheidole* sp *G* that showed a slight increase in winter. *M. delagoense* species produced a significantly larger body size in winter within infested areas and, in spring within cleared areas while *Pheidole* sp *A*, *Pheidole* sp *B* and *Pheidole* sp *G* showed no marked variations on both treatments within the two seasons. However, when further calculations were made to investigate if season contributed to species body size differences between treatments, paired t-test results showed no significant effect of season on ant species body size ($p < 0.05$, p-adjusted < 0.05, Table 2.5) except for *M. delagoense* which showed a significant increase in body size within cleared areas in spring compared to cleared areas in spring within infested areas. The small *M. delagoense* dominated infested and shaded treatments in spring because they were avoiding water loss; hence larger sized species dominated open areas because they lose less water.

Table 2.1: Ant species abundance in each of the six areas with increasing and decreasing time since *Chromolaena odorata* infestations and clearing in Hluhluwe-iMfolozi Park.

Functional group	Ant species	20 years infested	10 years infested	2 years infested	5 years cleared	2 years cleared	0 infested/ cleared	Total number	% Total number
Generalized myrmicinae	*Pheidole* sp *A*	35	1	0	16	5	5	62	6.83
Generalized myrmicinae	*Pheidole* sp *B*	18	38	2	9	7	9	83	9.15
Generalized myrmicinae	*Pheidole* sp *G*	9	8	57	5	72	60	211	23.26
Generalized myrmicinae	*Pheidole* sp *S*	0	0	2	0	0	0	2	0.221
Generalized myrmicinae	*Pheidole* sp *U*	0	0	0	4	0	0	4	0.44
Generalized myrmicinae	*Monomorium* sp *A*	15	0	0	10	0	1	26	2.86
Generalized myrmicinae	*Monomorium* sp *D*	5	19	2	2	4	0	32	3.53
Generalized myrmicinae	*Monomorium* sp *K*	0	7	0	0	4	0	11	1.21
Generalized myrmicinae	*Monomorium delagoense*	17	49	26	3	0	36	131	14.44
Hot/cold climate specialist	*Anoplolepis custodians*	4	33	0	1	139	1	178	19.63
Opportunist	*Tetramorium sericeventre*	0	5	7	1	0	0	13	1.433
Opportunist	*Tetramorium constancia*	1	12	0	7	0	8	28	3.08
Opportunist	*Tetramorium* sp *C*	9	0	0	21	0	6	36	3.96
Opportunist	*Tetramorium* sp *G*	0	7	0	0	0	0	7	0.77
Specialist predator	*Pletrotera*	0	6	0	0	0	0	6	0.66
Opportunist	*Myrmica natalensis*	33	30	0	0	0	14	77	8.48
	Total ants selected	152	209	96	79	231	140	907	100

Table 2.2: Mean ant diversity indices and species richness in each treatment. H' = Shannon-Weiner index (species diversity), S = total species, d = Margalef's index (species richness), and = Simpson's index (1– lambda).

	Infested treatment			**Cleared treatment**		
	20 years	**10 years**	**2 years**	**5 years**	**2 years**	**control**
S	11	11	6	11	6	9
d	1.99	1.87	1.09	2.28	0.92	1.62
H'(loge)	2.09	2.06	1.09	2.05	0.99	1.61
1-lambda	0.86	0.85	0.57	0.85	0.54	0.73

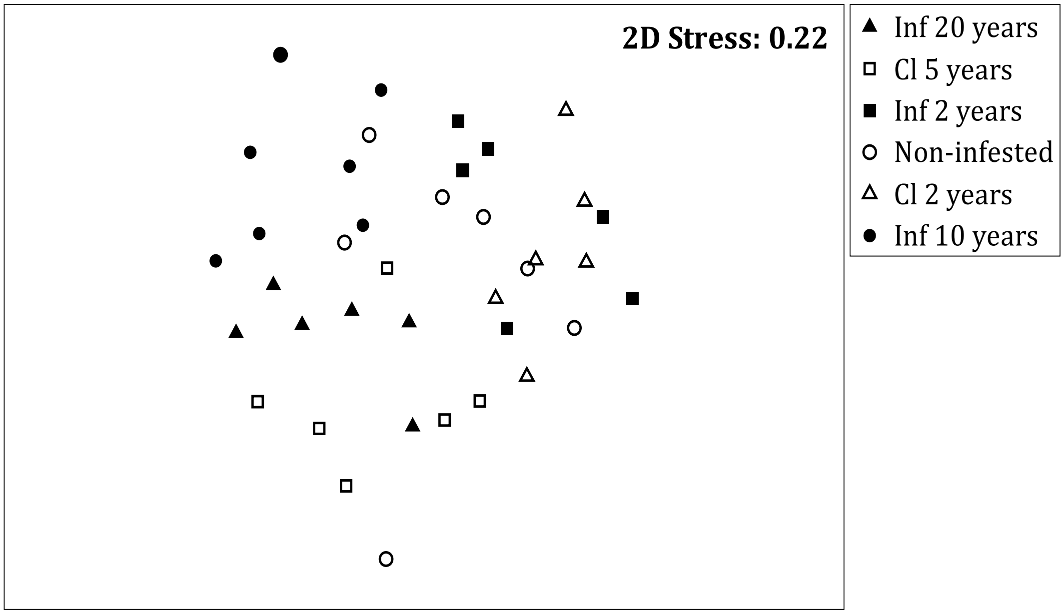

Fig 2.1: nMDS illustrating ant community composition in six treatments varying in *Chromolaena odorata* infestation and clearing.

Table 2.3: ANOSIM illustrating similarities between pairs of treatments. * denotes a significant difference.

	Test Statistic (R)	**Significance level (p)**
All treatments	**0.393**	**0.001**
Paired treatments		
10 yrs infested, 2 yrs cleared	0.754*	0.002*
10 yrs infested, non-infested	0.228	0.017
10 yrs infested, 2 yrs infested	0.548	0.004
10 yrs infested, 20 yrs infested	0.317	0.008
10 yrs infested, 5 yrs cleared	0.698	0.003
2 yrs cleared, non-infested	0.096	0.157
2 yrs cleared, 2 yrs infested	0.123	0.132
2 yrs cleared, 5 yrs cleared	0.709*	0.002*
2 yrs cleared, 20 yrs infested	0.620*	0.002*
non-infested, 2 yrs infested	-0.068	0.744
non-infested, 5 yrs cleared	0.271	0.020
non-infested, 20 yrs infested	0.224	0.026
2 yrs infested, 5 yrs cleared	0.830*	0.002*
2 yrs infested, 20 yrs infested	0.746*	0.002*
5 yrs cleared, 20 yrs infested	0.311	0.022

Table 2.4: Results from a SIMPER analysis indicating species contribution to closeness between the treatments in Hluhluwe-iMfolozi Park. Symbol: ° denotes species distinctive to a particular treatment.

	Average abundance (number of animals/ per trap/per session**)**	**Average Similarity**	**% contribution similarity**
Infested 20 years			
Pheidole sp *A*	2.170	13.740	30.450
Pheidole sp *B*	1.570	9.690	21.480
M. delagoense	1.400	7.330	16.240
M. natalensis°	1.670	6.150	13.620
Monomorium sp *D*	0.740	3.840	8.440
Infested 10 years			
Pheidole sp *B*	1.960	10.100	27.260
M. delagoense	2.470	17.810	48.100
Monomorium sp *D*	1.050	1.800	4.870
A. custodians°	1.360	2.570	6.930
T. constancia	0.790	1.630	4.390
Infested 2 years			
Pheidole sp *G*	2.940	41.560	87.250
M. delagoense	1.410	5.250	11.040
Non-infested			
Pheidole sp *B*	0.610	2.050	7.010
Pheidole sp *G*	2.130	14.600	49.920
M. delagoense	1.630	9.900	33.860
Cleared 5 years			
Pheidole sp *A*	1.410	11.430	26.660
Pheidole sp *B*	0.970	5.570	13.000
Pheidole sp *G*	0.690	2.800	6.530
Monomorium sp *A*	0.980	5.830	13.610
T. constancia	0.630	2.400	5.590
Tetramorium sp *C*°	1.620	11.729	27.330
Cleared 2 years			
Pheidole sp *A*	0.640	3.930	8.310
Pheidole sp *B*	0.760	3.200	6.780
Pheidole sp *G*	3.290	37.76	79.910

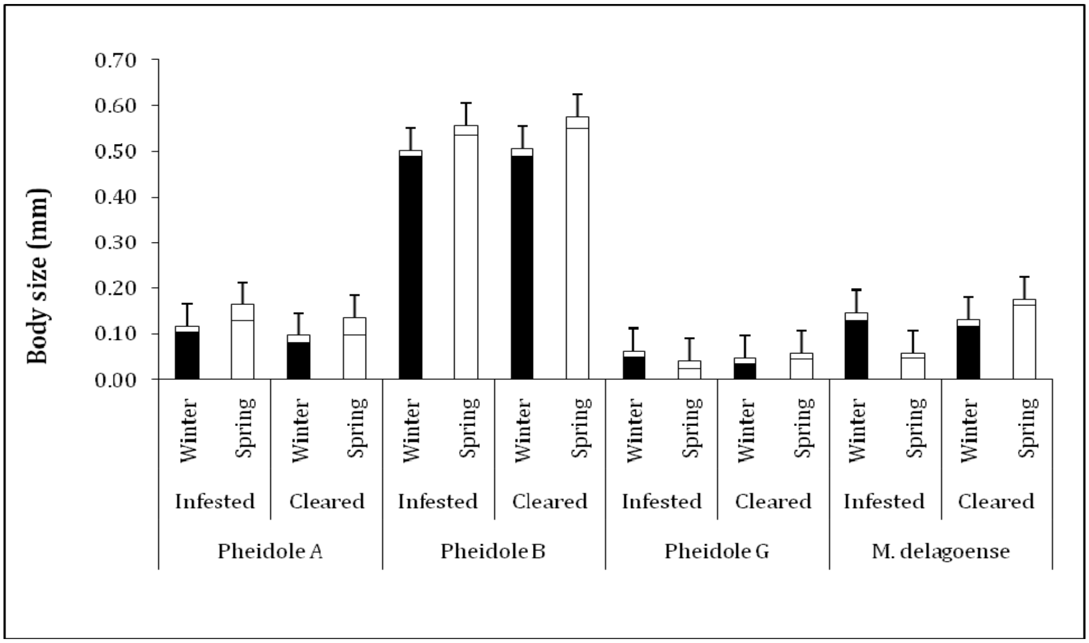

Fig 2.2: Three-way ANOVA illustrating ant body size response of each species to variations in seasons and treatments.

Table 2.5: Multiple two-tailed t-test for differences between cleared and infested areas during each season and for each species.

Species	Season	df	t-value	p- adjusted
M. delagoense	Spring	44.851	-6.6294	2.938400e-07*
M. delagoense	Winter	12.539	0.3121	8.686857e-01
Pheidole sp A	Spring	3.877	0.6156	8.097333e-01
Pheidole sp A	Winter	31.057	1.4931	3.880000e-01
Pheidole sp B	Spring	12.062	-0.5276	8.097333e-01
Pheidole sp B	Winter	38.676	-0.0029	9.977000e-01
Pheidole sp G	Spring	32.473	-1.6958	3.880000e-01
Pheidole sp G	Winter	56.619	1.0759	5.732000e-01

Discussion

Ant community: abundance and diversity

Seasonal variations influence ant movement through temperature changes and productivity of plants. Ants inhabit warm regions that are frost-free (Holldobler & Wilson 1990). Extremely hot temperatures can be dangerous for them, thus ants can escape such areas by hiding in nests during the day (Andersen 1995) and are positively associated with non-monotypic vegetation. In this study, ants showed greater diversity and increase in their abundance in spring than in winter. Decrease in ant diversity and abundance in winter is attributable to cold temperatures that may have caused ant inactivity during this season. The lack of wet soil in winter hinders vegetation germination, thus food is limited and population reduction is experienced. In agreement with other studies, my results suggest that a higher diversity of vegetation in spring may provide ants with more numerous foraging places and food. In spring, vegetation is diverse as climate and rainfall favours germination. However, seasons had no effect on ant body size, suggesting that the effect of season may be directly related to activity rather than to actual changes in resident ant communities.

The study showed that the presence of *C. odorata* infestation and its dense structure did not seem to affect ant communities. However, although the results were not significant, the old infested treatments contained a higher abundance of generalist species compared to other treatments, implying that some habitat disturbance did occur and it led to increased generalist species of *Tetramorium*, *Pheidole*, *Monomorium* and *Myrmica*. These species are highly competitive for resources and may have attributed to absence or low abundance of other species. According to Murdoch & Oaten (1975), areas that contain structurally dense vegetation have greater surface area which provides hiding place for prey and reduces competition among coexisting species. Furthermore, the cleared treatments did not show rehabilitation of state shift of the previously infested sites as no diversity and abundance of species was confirmed. The results suggest that rehabilitation may take longer in time to show any significant change in ants. However, the findings from this study differ from previous researches assessing *C. odorata* effect on biodiversity in HiP that showed a significant increase of species with *C. odorata* removal (Julius 2007; Dumalisile 2008; Mgobozi *et al*. 2008).

To conclude, seasonal variations had a stronger influence on ant communities compared to invasions of *C. odorata*. However, it should be noted that other environmental factors such as differences in soil type may have played a role in influencing ant distribution. I therefore suggest that these factors should be included in future studies on the effects of plant invasions on biodiversity.

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CHAPTER 3

Response of ant communities to variation in rainfall, grazing intensities and grass types

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Abstract

Studies assessing the ecological impacts caused by ungulate grazing are of great importance for the management and conservation of species. Modifications in grasslands by ungulate grazing may have drastic effects on fauna assemblages through changes in habitat structure, diversity and microclimate. Ants are ecologically dominant invertebrates in terrestrial systems and are therefore often used as ecological indicators. The aim of this study was to examine differences in ant communities in relation to variations in grazing intensity, grass height stature and grass type within two regions receiving varying rainfall. Ants were sampled in eight exclosures in two regions of the Hluhluwe-iMfolozi Park, South Africa, that differ in both altitude and rainfall: Hluhluwe and iMfolozi. Within each region, exclosures were located in four grass types (lawn, tall, mixed bunch and mixed short grass) and each exclosure included three grazing treatments (unfenced, accessible to all herbivores, fenced to exclude mega-herbivores, and fenced to exclude all herbivores). Humidity, grazing and grass type interacted in their effects on ant abundance. For ant species richness and diversity, on the other hand, the effect of grazing was not influenced by humidity and grass type, but humidity and grass type influenced each other in their effects on species richness and diversity. In Hluhluwe, differences in ant composition only occurred in lawn and mixed short grass, while other treatments were similar. In iMfolozi on the other hand, there were no differences among any of the treatments in ant species composition but species abundance differed between treatments. To conclude, whereas the effect of grazing on ant abundance was influenced by both humidity and grass type, its effect on ant diversity and richness was uniform across habitats, indicating that population dynamics of ant communities are influenced by a combination of humidity, grass type and grazing.

Introduction

Worldwide, conservationists have highlighted the necessity to understand factors influencing the increased rate of species extinction and decline, including studies monitoring the effects of ecological changes. African savannas are significant in terms of plant, animal and human wellbeing (Caro 1999; Smith *et al.* 2000). The abundance of grasses and trees in these systems provide nesting and food to a wide variety of organisms. However, productivity and heterogeneity of savanna systems are changing due to a wide variety of activities such as cultivation, burning, and alien plant invasions and herbivory by both domestic and wild animals. This causes modification in species composition and abundance.

The diversity within savanna ecosystems is primarily regulated by rainfall and grazing (Klop & Prins 2008), although some studies have suggested that grazing may have less impact than rainfall (Westoby *et al*. 1989; O'Connor 1994). Moreover, the effects of grazing on biodiversity have not been easy to generalize due to different species specific responses. However, many studies have revealed that biodiversity is enhanced by light grazing as old and monotonous grass is replaced by heterogeneous food and nesting areas (Read & Andersen 2000; Littlewood 2008; Ogada *et al*. 2008), while absence of grazing has negative consequences for biological diversity, resulting in species decline due to lack of vegetation variety (McNaughton 1984; Hartnett *et al*. 1996). However, persistent utilization of grass by ungulate herbivores has shown to benefit unique herbivore communities, and has therefore been classified as important for conservation of biological diversity (Olff & Ritchie 1998; Littlewood *et al*. 2006; Krook *et al*. 2007; Mgobozi *et al*. 2008). In contrast, reductions in vegetation cover in overly grazed areas have been shown to have negative consequences for diversity and population increase of certain animal assemblages (Abensperg-Traun *et al*. 1996; Bestelmeyer & Wiens 1996; Keesing 1998; Pöyry *et al*. 2006).

Since the use of indicators often is less costly than monitoring a complete system, a wide variety of ecological indicators have been identified to monitor environmental impacts (Gardner 2010). One of the most used taxonomic groups of terrestrial indicators is ants. Ants are one of the most numeric groups of invertebrates that populate warm terrestrial environments. They interact with a wide variety of organisms ranging from the lowest trophic level to large carnivores (Holldobler & Wilson 1990). Ants are involved in many ecosystem functions including nutrient formation, pollination, granivory and herbivory, and are sensitive to ecological changes. Ants are also an important food source for many organisms. Their diversity and abundance is linked to vegetation quantity, microclimate and soil type (Hoffman 2010). Therefore, ants can influence vegetation survival and reproduction through pollination and seed dispersal to sites suitable for seed growth (Holldobler & Wilson 1990). Since ants are ecologically dominant species, the obstruction of their services could have negative consequences to botanical and fauna community composition (Evans *et al*. 2006). Furthermore, immediate response of ants to disturbances makes them ideal as reliable indicators of environmental change.

The Hluhluwe-iMfolozi Park, hereafter referred to as HiP, is a large conservation area situated in south eastern part of South Africa. The use of grazing for management of the flora in HiP has a long history, and has resulted in the production of two common grass types: lawn grass and tall bunch grass. Lawn grass is produced when tall bunch grass is frequently trimmed by herbivores. In HiP, this grass type is sustained mostly by white rhinoceros *Ceratotherium simum*, whereas tall grass is maintained by fire (Archibald *et al.* 2005). Lawn grass grows unique grass species. It therefore differs in structure and composition from other grass types and is subsequently inhabited by many endemic animal species (Krook *et al*. 2007; Mgobozi *et al*. 2008). The changes in grassland structure and composition affects the stability of ecological services as species are eliminated or abandon the habitat as preferred grass types are removed during grazing.

In the current study, the effects of rainfall, grazing intensity and grass types on ant communities was investigated in HiP. The study also compared ant diversity, richness and abundance between different grass types found in HiP. The information from the study will help devise appropriate grazing management strategies, and increase heterogeneity in ecosystems.

The study evaluated the effects of grazing intensity and grass type on ant abundance, species richness and diversity within two regions experiencing different rainfall. The study objectives were (a) to determine if ant abundance, species richness and diversity change in relation to different grazing levels (heavily grazed, lightly grazed and non-grazed), (b) to investigate if ant number, species richness and diversity vary in relation to grass type (c) to investigate if lawn grass supports a unique species and if ant abundance, species richness and diversity is greater compared to tall grass (d) determine if the high altitude and high rainfall area of Hluhluwe has higher ant abundance, species richness and diversity compared to the low altitudinal and low rainfall area of iMfolozi. It was hypothesized that the presence of heterogeneous flora will attract a higher diversity and abundance of ants in Hluhluwe due to the availability of more diverse resources. Because ants often forage in open areas, they were expected to be more abundant in moderate and heavily grazed areas and in less dense grass types.

Materials and methods

Exclosure and experimental set-up

Ants were collected in spring season in the month of September in 2005 (Mgobozi *et al.* 2008), a season when ant foraging is high compared to other seasons. Ants were sampled in eight exclosure plots that have been in Hluhluwe-iMfolozi Park since 1999 (Staver *et al*. 1999). Of these, four exclosure plots were located in Hluhluwe, which lies in the northern part of the park and is a high precipitation area, and the other four were located in the low precipitation area of iMfolozi, which is in the southern part of the park. Within each region, sites were demarcated into four grass types; one mixed bunch grass, one mixed short grass, one lawn grass and one tall bunch grass (Fig 3.1). In both regions, each of the exclosure plots was divided into three replicate sites (40 m x 40 m, n = 24 sites) which differed based on the extent of grazing pressure put by herbivores. The grazing treatments were unfenced sites, which were accessible to all herbivores, fenced sites which excluded grazers such as white and African elephant (*Loxodonta Africa)*, and sites fenced with mesh excluding all animals starting above the size of shrub hare (*Lepus saxatilis)*.

Within each of the 24 sites, sampling was done through 10 pitfall traps spaced 2 m apart in a rectangular grid of 2 m x 8 m. The pitfall trap method was used because it gives a true representation of the importance of species foraging on the ground and because the method is easy to use. Small smooth-sided plastic jars that were partially filled with 2 cm 50/50 mixture of water/ propylene glycol and few drops of liquid soap were submerged, to their brim, into the ground and were left out for 72 hours in the field.

After collection, ants were separated from other invertebrates and were kept inside small specimen bottles partially filled with 70 % ethanol. Ant classification was confirmed using preserved reference specimens.

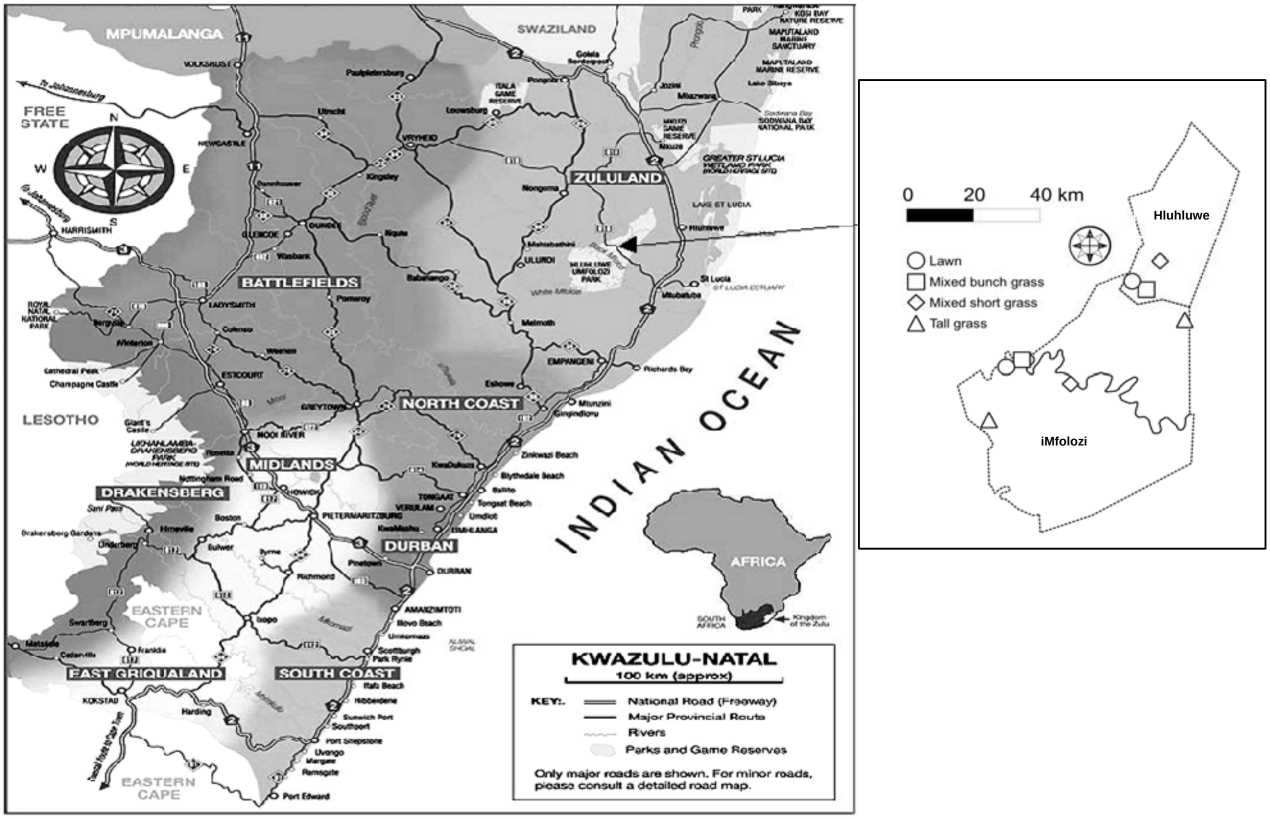


Fig 3.1: Map showing grazing exclosures located in Hluhluwe and iMfolozi sections in Hluhluwe-iMfolozi Park.

Statistical analysis

To investigate similarities between treatments with regards to ant species composition, raw data on ant abundance in each trap was square root transformed and Bray-Curtis Rank similarity matrices were calculated using PRIMER version 6. The similarity matrices were used to graphically illustrate similarities in ant community structure and composition using non-parametric Multidimensional Scaling (nMDS). In nMDS, points that occur close to each other have more similar species composition than points that are further apart. In addition, Analysis of Similarity (ANOSIM) was used to examine if there were similarities in ant species composition between treatments. In ANOSIM, treatments are similar if their global R = 0 and differ when R = 1. If any differences or similarities existed between treatments, a Similarity Percentage test was further used to examine species that contributed to the similarities or differences.

To investigate the effects of region, grazing level and grass type on ant diversity, three separate diversity indices were calculated. First, a Shannon-Weinner index which focuses on examining species heterogeneity and abundance of less common species in a sample, was calculated as $H' = -\Sigma p_i \log_{10} p_i$, where p_i is the proportion of the total number of ants found in one trap that belong to species i. Second, Margalef's index, which examines the number of species present for a given number of individuals (species richness) was calculated as $d = S\text{-}1 / \log N$ where S is the number of species and N is the number of individuals trapped. Finally, Simpson index, which focuses on measuring abundance of common species, was calculated as $\lambda = \sum p_i^2$, where p_i is the proportions of the total number of ants found in one trap that belong to species i. All indices were calculated using Primer version 6 on each individual trap of each exclosure and summarized for each treatment within each exclosure.

Generalized linear models with a poisson error structure and a log link function were used to evaluate the effects of region, grazing level and grass type on ant abundance and species richness. In the first model, raw number of ants collected in each trap was used as response variable, and region (Hluhluwe or iMfolozi), grazing level, grass type and all interaction terms were added as fixed effects. A similar generalized linear model was used to evaluate the effects of region, grazing level and grass type on ant species richness. This model had the same fixed effect structure as described above, but instead of raw number of ants it used number of ant species as response variable. Furthermore, Analyses of variance was used to evaluate the effects of region, grazing level and grass type on each of the three diversity indices. Each of these three models had the same fixed effect structure as described above, and each diversity index as response variable, respectively.

Results

Ant community composition in Hluhluwe and iMfolozi

A total of 20 ant species were identified (Appendix A), 18 species in the Hluhluwe region and 10 species in iMfolozi. The most prominent group in the Hluhluwe region was dominated by the genus *Pheidole* (seven species) followed by *Monomorium* (four species) and the genus *Tetramorium* (three species). *Myrmica natalensis*, *Anoplolepis custodians*, and one unknown species were the least abundant species. In iMfolozi, the genus *Pheidole* and *Monomorium* were the most dominant with three species each, followed by *Tetramorium* (two species), *Anoplolepis custodian* and one unknown species. Overall, the Hluhluwe region contained 58 % of relative ant abundance compared to 42 % in iMfolozi. The most dominant species in Hluhluwe region was *M. delagoense* (30.4 %) followed by *Anoplolepis custodians* (18.9 %) and 16.5 % for *Pheidole* sp *G*., while iMfolozi was dominated by *M. delagoense* (53 %), *Pheidole* sp *G* (18.4 %) and then *A. custodians* (17.6 %). The most frequently encountered genera in all plots were *Monomorium* (46.1 %) followed by *Pheidole* (28.6 %), *Anoplolepis* (18.4 %), *Tetramorium* (4.79 %) and *Myrmica* (2.0 %). Out of the three grazing gradients, heavily grazed plots contained least of all ant individuals (23.0 %), while the lightly grazed plots produced the largest ant abundance of individuals (43.6 %) followed by non-grazed (33.4 %).

There were similarities in ant community composition both within a grass types and within grazing levels (Fig 3.2a, b). The nMDS for Hluhluwe showed that differences in ant composition only occurred in lawn grass and mixed short grass, while other treatments were similar. In iMfolozi, nMDS showed that there were no differences in ant species composition but species abundance differences between treatments and site existed. In addition, there were differences between treatments in Hluhluwe and iMfolozi with regards to similarities in ant species composition (ANOSIM: Global R = 0.338, *P* = 0.001; Global R = 0.27, *P* = 0.002, Appendix B). In Hluhluwe, differences existed between the pairs of tall none and tall light exclosures, tall none and lawn light, tall none and mixed short none, tall light and mixed short none, tall light and mixed short light, tall light and mixed short heavy, mixed bunch light and mixed short none, mixed bunch heavy and mixed short light, lawn heavy and mixed short none (Appendix B, Hluhluwe). In iMfolozi, mixed bunch none and tall heavy, mixed bunch light and tall heavy and mixed bunch heavy and tall heavy exclosures showed differences in community composition (Appendix B, iMfolozi).

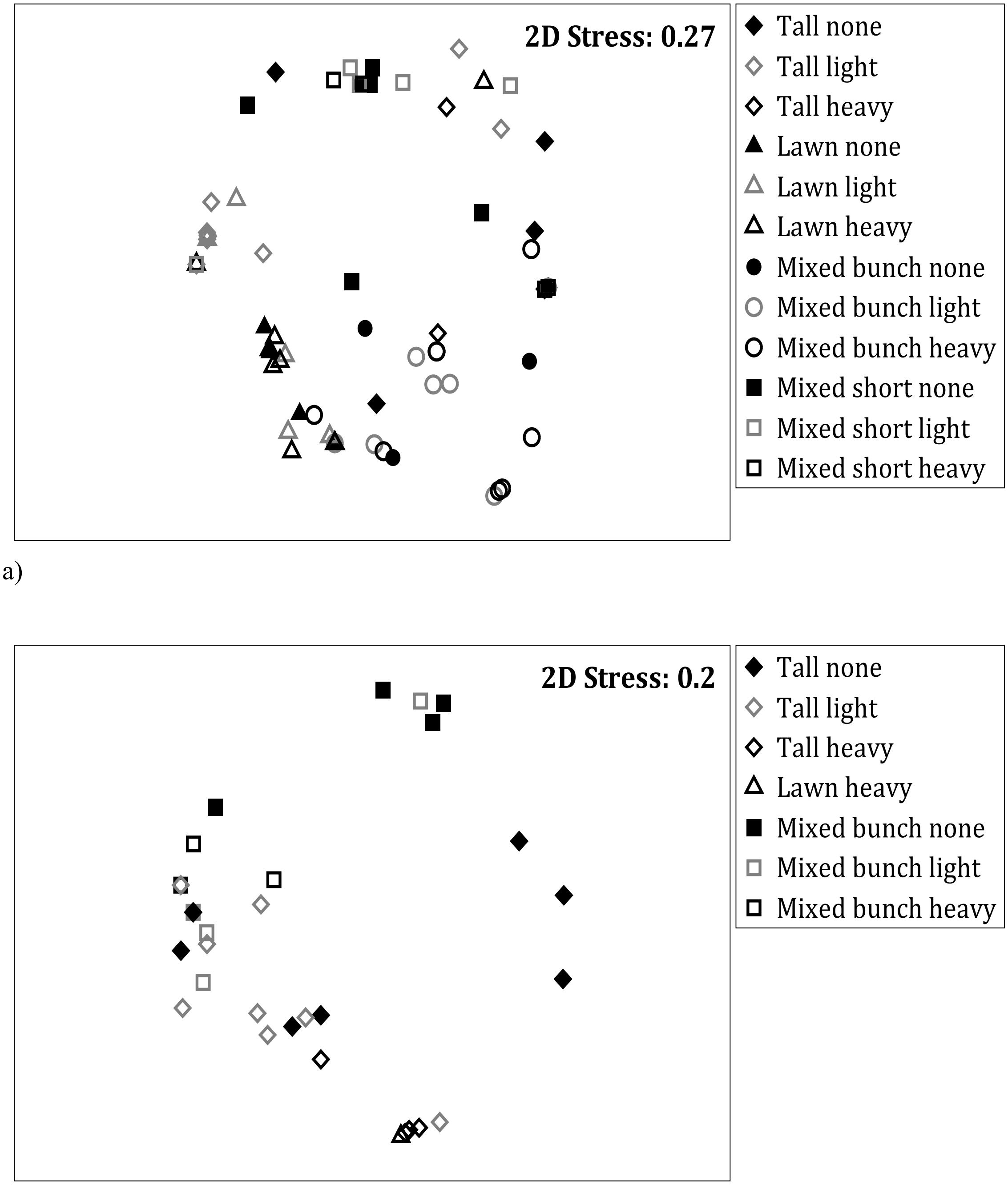
In Hluhluwe, mixed short grass and tall grass with heavy and no grazing contained unique species of *Monomorium* sp *A* and *Pheidole* sp *P*, *M. natalensis* and *Pheidole* sp *A*, while mixed bunch grass contained unique species of *Pheidole* sp S. Lawn grass and mixed bunch grass were dominated by *M. delagoense*. This species decreased where grazing was practiced, when other species such as *A. custodians* occurred in higher abundance. In iMfolozi, mixed bunch grass and tall grass with no grazing contained unique species of *A. custodians*, *T. constancia* and *Pheidole* sp *A* (Appendix C). *M. delagoense* was shared between tall grass with no grazing, mixed bunch grass with no grazing and mixed bunch grass with heavy grazing sites. Lawn grass in both Hluhluwe and iMfolozi contained no unique ant species opposing what previous literature had suggested about this grass type.

Ant abundance, species richness and diversity within grazing levels and grass types in the two regions of the Hluhluwe-iMfolozi Park

There was a significant three-way interaction effect of grazing level, reserve and grass type on ant abundance ($F_{2,\ 240} = 23.13$, $P < 0.001$). While the highest ant abundance occurred in lightly grazed areas in tall grass types in iMfolozi, there was generally higher ant abundance in Hluhluwe (Fig 3.3 a, b). Whereas the differences between grazing levels was consistent between Hluhluwe and iMfolozi in the tall grass type, they differed both in the lawn grass and in the mixed bunch grass. No ants were found in any plots in the mixed short grass in iMfolozi. The lightly grazed exclosures had the highest ant abundance within all grass types in Hluhluwe except for the lawn grass which had the highest abundance in non-grazed and heavily grazed (Fig 3.3a).

In iMfolozi, lightly grazed plots in tall grass had the highest ant abundance followed by non-grazed plots in mixed bunch grass. Mixed short and lawn grass had lower ant abundance within all grazing levels than both mixed bunch and tall grass (Fig. 3.3b). There was a significant interaction effect of region and grass type on ant species richness ($F_{3,\ 240} = 55.253$, $P < 0.001$; Fig 3.4) and a main effect of grazing ($F_{3,\ 240} = 17.812$, $P < 0.001$). There was not a significant three-way interaction effect ($F_{6,\ 240} = 3.571$, $P = 0.734$). Species richness was consistently higher in Hluhluwe than in iMfolozi (Fig 3.4a, b). In Hluhluwe, the highest species richness was found in heavily grazed lawn grass and in lightly grazed mixed bunch grass (Fig. 3.4a). In iMfolozi, the highest species richness was found in tall grass followed by mixed bunch and then lawn and mixed short grass (Fig 3.4b).

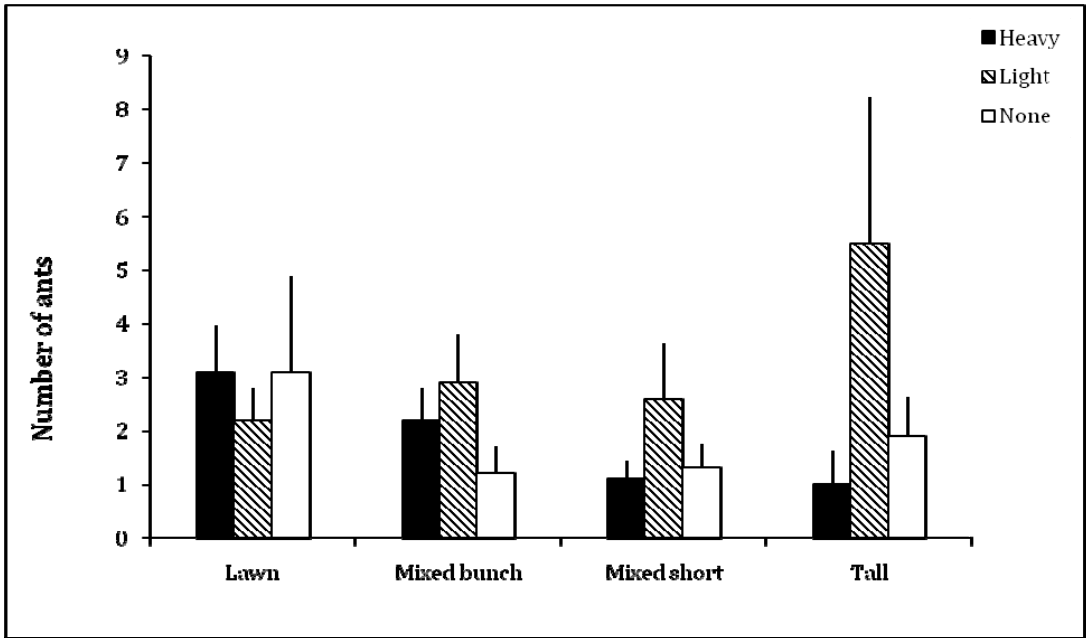
There was a significant interaction effect of region and grass type on both ant species diversity (Shannon Weiner index: $F_{3,\ 240} = 4.45$, $P = 0.004$), richness (Margalef's indices: $F_{3,\ 240} = 2.814$, $P = 0.04$) and evenness (Simpson' indices $F_{3,\ 240} = 3.781$, $P = 0.011$). There was not a significant three-way interaction for any of the three indices (Shannon-Weiner index: $F_{4,\ 240} = 0.198$, $P = 0.939$, Margalef's index: $F_{4,\ 240} = 0.363$, $P = 0.834$, Simpson's index: $F_{4,\ 240} = 0.341$, $P = 0.850$).



a)

b)

Fig 3.2: Multi-dimensional Scaling graphically ranking grazing gradients (heavily grazed, lightly grazed and non-grazed exclosures) and grass types based on similarities in ant community composition in Hluhluwe (a) and iMfolozi (b) sections in Hluhluwe-iMfolozi Park.



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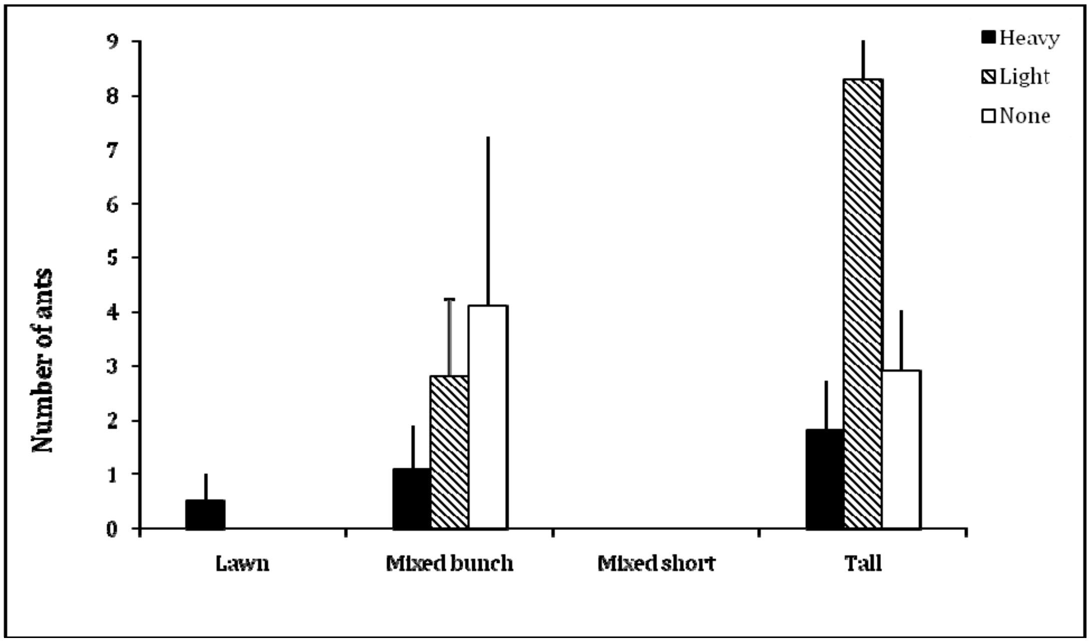
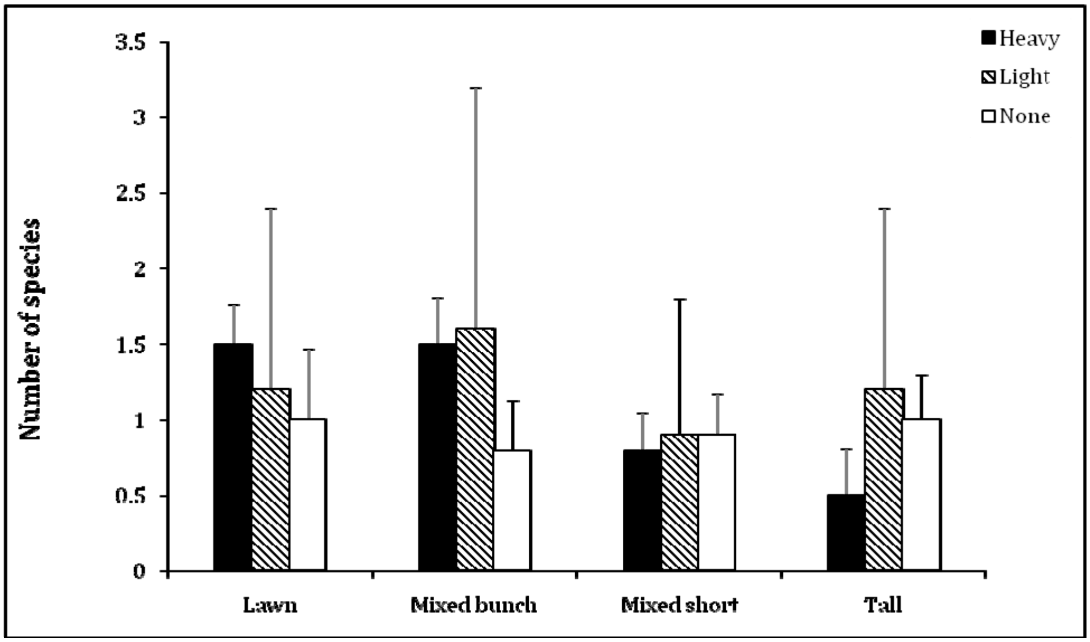
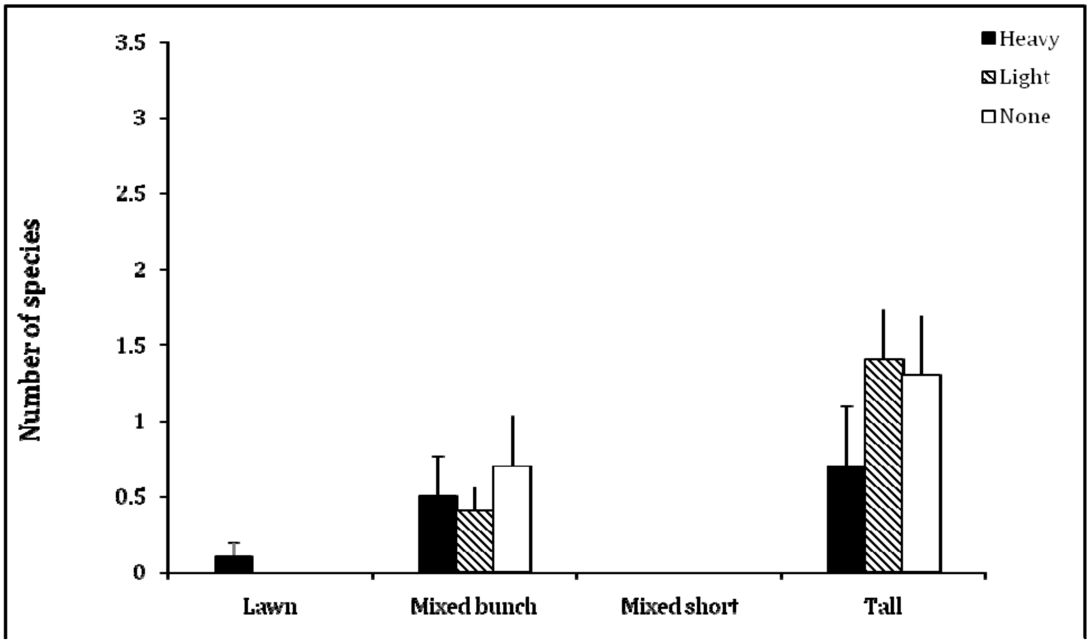


b)

Fig 3.3: Ant abundance within each grazing level and grass type in Hluhluwe (a) and iMfolozi (b) sections in Hluhluwe-iMfolozi Park, South Africa.



a)



b)

Fig 3.4: Ant species richness within each grass type in Hluhluwe (a) and iMfolozi (b) sections in Hluhluwe-iMfolozi Park, South Africa.

Within Hluhluwe, the highest ant diversity, richness and evenness was found in mixed bunch grasses followed by lawn grass and then tall grass and then mixed short grass (Fig 3.5a-c). The iMfolozi region, on the other hand, had the highest diversity, richness and evenness in tall grass followed by mixed bunch grass (Fig 3.5d-f).

Discussion

It was hypothesised that higher rainfall areas would produce greater ant abundance, species richness and diversity as a result of high vegetation growth and plant diversity that attract more ants. My results confirmed these predictions, with generally higher ant abundance, species richness and diversity in the warmer and more humid Hluhluwe compared to the cooler and the dryer iMfolozi region. However, ant abundance was influenced by the interaction of rainfall, grass type and grazing level whereas ant diversity and species richness influenced by an interaction of grass and humidity. Grazing also had an effect on species richness and diversity, but in contrast to its effect on abundance it was not modified by grass type or humidity. Grazing also had an effect on species richness and diversity, but in contrast to its effect on abundance it was not modified by grass type or humidity. Grazing produced higher ant abundance in lightly grazed exclosures in both lower and higher rainfall regions in tall grass types. However, the highest ant abundance in light grazed areas in tall grass was obtained in the lower humidity region not the higher humidity region, suggesting that mild humidity in light grazing in tall grass type promoted flora growth and that the thickness in grass cover in tall grass type protected ants against dehydrating temperatures in spring. The lower ant abundance in higher humidity Hluhluwe region compared to the lower humidity iMfolozi region in light grazed exclosures in tall grass type is attributed to exposure to high temperature conditions temperatures which may have led to ant inactivity. The most dominant species in iMfolozi in light grazed exclosures in tall grass was the *M. delagoense*. The high abundance in *M. delagoense* in iMfolozi is expected as this species thrives under all environmental conditions. The abundance of *M. delagoense* is attributed to less competition from other species that were eliminated by unfavourable environmental conditions. In contrast, *A. custodians* dominated Hluhluwe in light grazed exclosures in the tall grass. *A. custodians* are omnivorous and highly competitive species that occupy disturbed, open and well-insulated areas (Addison & Samways 2006).

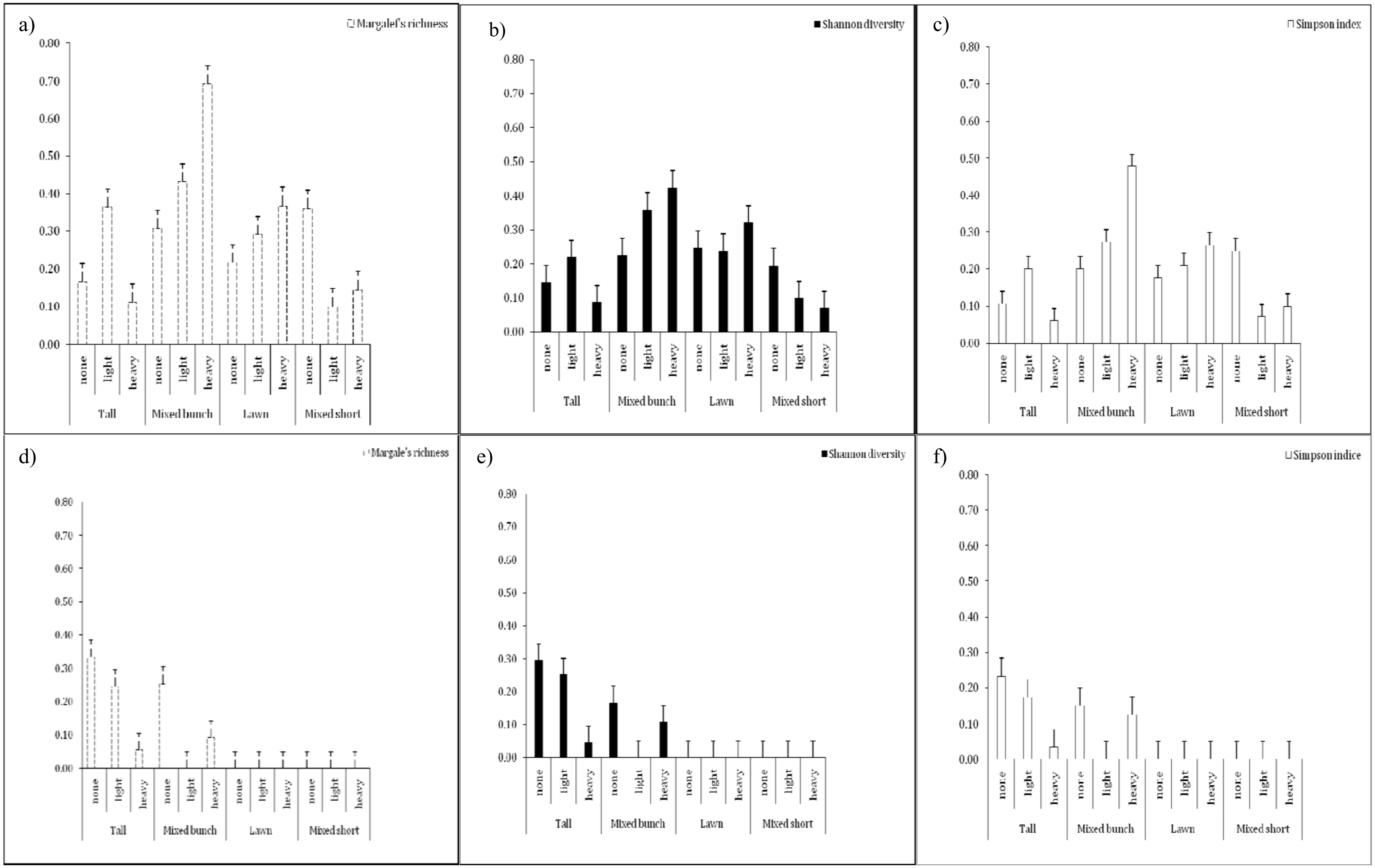


Fig 3.5: Ecological diversity indices showing ant communities in different grazing levels and grass types in Hluhluwe (a-c) and iMfolozi (d-f) regions in Hluhluwe-iMfolozi Park.

The high abundance of *A. custodians* in lightly grazed exclosures in tall grass type is attributed to habitat modification caused by herbivory and decreased competition from other species, and high vegetation cover that provided high insulation for this species. Decrease in *A. custodian* number in other grass types such as lawn grass in Hluhluwe could be attributed to less insulation and probably predation. However, the absence of *A. custodians* in iMfolozi in tall bunch grass in light grazed exclosures could be caused the presence of other competitive species, and its abundance in mixed bunch grass and low abundance of *T. constancia* in the same grass and grazing level revealed this species as a solitary species and a superior competitor.

In contrast to abundance, ant diversity and species richness, grazing level factor had no influence of humidity and grass type, but the combination of humidity and grass type regulated ant diversity and species richness. Spatial variations in rainfall influenced mineralization and growth of vegetation thereby affecting distributions in ant species diversity and richness. Ant diversity increased in areas that have high humidity and forage diversity whereas low humidity areas obtained low ant species diversity and richness. An increase in soil moisture in high rainfall area of Hluhluwe and mineralisation could have promoted growth of nutritional rich forage that attracted different species of ants in the high humidity region, whereas low rainfall resulted in diminished growth of vegetation thereby eliminating species that require heterogeneity in vegetation in iMfolozi. Findings from this study are similar to Warui (2004) in Kenya, Laikipa, where increase in rainfall amounts were positively correlated to high spider diversity and high vegetation production within exclosures and, Levings & Windsor (1996), who confirmed insect quantity increase in moist environments because these areas produce high food abundance compared to dry areas.

However, these effects of humidity differed between grass types, with more pronounced differences between grass types in the arid iMfolozi compared to Hluhluwe. The lawn and mixed short grass types obtained the lowest ant diversity and species richness in the arid iMfolozi compared to other grass types, indicating less survival resources nesting sites and food, and harsh conditions due to less covered habitat. The high ant heterogeneity in mixed bunch and tall grass is attributed to enough resources and protecting against cool weather. In contrast to iMfolozi, higher ant diversity and richness in Hluhluwe mixed bunch and lawn grass showed enhanced plant germination, diversity and cover in mixed bunch grass. The increase in vegetation cover in mixed bunch grass served as a barrier to hot temperatures during this season; and probably resulted in ants decrease in open lawn than mixed bunch, even though not significant. However, decrease in ant diversity in tall grass and mixed grass maybe due to lack of vegetation variety compared to other grass types and geological factors in mixed short grass (see Fig 3.1, Hluhluwe region). The high ant diversity and richness is lawn and mixed grass suggested the importance of heterogeneity in habitat for long-term management of biodiversity. In addition, promotion of ant variety and richness in the presence of high rainfall in lawn grasses which are formerly regarded as anti-conservation due to focused trimming by herbivores showed that these grasses are worth to be maintained and conserved in savannas in high rainfall regions. However, maintenance of these grass types in cool temperate and low rainfall regions seem to be less important for ant species conservation.

In conclusion, this study showed that humidity, grazing and grass type interacted in their effects on ant abundance, but that only humidity and grass type interacted in their effect on ant diversity. There was, however, an effect of grazing on ant diversity, but this effect was not altered by humidity or grass type. My result generally supported a higher abundance and diversity in the more humid Hluhluwe compared to the arid iMfolozi, which highlight the importance of humidity for ant communities. Moreover, the high ant diversity and species richness is lawn and mixed grass suggested that the heterogeneity within habitats is critical for long-term management of biodiversity. Finally, this study showed complex interactions between habitat, herbivory and climate variables in the effects on ant communities, and also that these interactions differed between effects on abundance versus effects on diversity.

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Appendix A: Raw data of ant species in each trap in each region, grazing level and grass type in a study area of Hluhluwe-iMfolozi Park. Symbol (-) denotes not present.

Reserve	**Grazing level**	**Grass type**	***Species***	**Number of ants**
Hluhluwe	Non-grazed	Tall grass	*Pheidole sp G*	2
			-	-
			Myrmica natalensis	2
			Pheidole sp T	1
			Pheidole sp G	1
			Tetramorium sp F	1
			Pheidole sp G	4
			Myrmica natalensis	2
			-	-
			Myrmica natalensis	4
			Monomorium delagoense	1
			-	-
			Pheidole sp G	1
Hluhluwe	Lightly grazed	Tall grass	*Anoplolepis custodians*	28
			Anoplolepis custodians	1
			Myrmica natalensis	1
			Tetramorium sericeventre	1
			Unknown	1
			Anoplolepis custodians	4
			Anoplolepis custodians	6
			-	-
			Anoplolepis custodians	7
			Anoplolepis custodians	3
			-	-
			Anoplolepis custodians	1
			Pheidole sp H	1
			Pheidole sp S	1
Hluhluwe	Heavily grazed	Tall grass	-	-
			-	-
			Pheidole sp A	3
			-	-
			-	-
			-	-
			Pheidole sp G	1
			Monomorium delagoense	1
			Pheidole sp G	4
			Pheidole sp A	1
			-	-
			-	-
Hluhluwe	Non-grazed	Mixed grass	*Pheidole sp G*	1
			Monomorium delagoense	2
			Anoplolepis custodians	1
			Pheidole sp S	2
			Pheidole sp G	1
			-	-
			Pheidole sp G	1
			-	-
			-	-
			-	-
			Pheidole sp S	3
			Monomorium delagoense	1
			-	-
Hluhluwe	Lightly grazed	Mixed grass	*Pheidole sp G*	1

			-	-
			Monomorium delagoense	3
			Pheidole sp S	1
			Monomorium delagoense	1
			-	-
			Monomorium delagoense	1
			Pheidole sp G	3
			Pheidole sp S	2
			Pheidole sp S	4
			Monomorium delagoense	4
			Pheidole sp G	2
			Pheidole sp B	1
			Pheidole sp G	1
			Monomorium delagoense	2
			Pheidole sp S	1
			-	-
Hluhluwe	Heavily grazed	Mixed grass	*Pheidole sp S*	2
			Pheidole sp S	1
			Myrmica natalensis	3
			Pheidole sp P	1
			Pheidole sp S	2
			Monomorium delagoense	2
			Pheidole sp S	1
			-	-
			Pheidole sp G	1
			Monomorium delagoense	1
			Pheidole sp G	1
			Myrmica natalensis	1
			Monomorium delagoense	4
			Pheidole sp A	1
			Pheidole sp G	1
			Monomorium delagoense	1
			-	-
Hluhluwe	Non-grazed	Lawn grass	*Monomorium delagoense*	3
			Pheidole sp H	2
			-	-
			Monomorium delagoense	1
			Monomorium delagoense	7
			Tetramorium sericeventre	1
			Pheidole sp A	4
			Anoplolepis custodians	5
			-	-
			-	-
			-	-
			-	-
			Monomorium delagoense	6
			Anoplolepis custodians	1
			Anoplolepis custodians	1
			-	-
Hluhluwe	Lightly grazed	Lawn grass	*Anoplolepis custodians*	2
			Monomorium sp K	1
			Unknown	1
			-	-
			Anoplolepis custodians	3
			Monomorium delagoense	2
			Anoplolepis custodians	1
			Monomorium delagoense	2
			Monomorium delagoense	2
			Monomorium delagoense	1
			-	-

			Tetramorium sericeventre	3
			Monomorium delagoense	3
			Monomorium delagoense	1
Hluhluwe	Heavily grazed	Lawn grass	*Unknown*	1
			Anoplolepis custodians	1
			Anoplolepis custodians	1
			Monomorium delagoense	3
			Anoplolepis custodians	3
			Monomorium delagoense	4
			Anoplolepis custodians	1
			Monomorium delagoense	3
			Pheidole sp B	2
			Monomorium delagoense	1
			Monomorium delagoense	1
			Anoplolepis custodians	2
			Monomorium delagoense	1
			-	-
			Monomorium delagoense	6
			Tetramorium constancia	1
Hluhluwe	Non-grazed	Mixed grass	*Monomorium sp A*	3
			Monomorium delagoense	1
			Monomorium sp A	3
			Monomorium sp A	1
			Monomorium sp D	1
			-	-
			-	-
			-	-
			Monomorium sp A	1
			Monomorium sp A	1
			Pheidole sp G	1
			Pheidole sp H	1
			-	-
Hluhluwe	Lightly grazed	Mixed grass	-	-
			Anoplolepis custodians	1
			Monomorium sp A	6
			Monomorium sp D	2
			Monomorium sp A	3
			Pheidole sp P	5
			-	-
			-	-
			Monomorium sp A	1
			Pheidole sp P	6
			Pheidole sp G	1
			-	-
Hluhluwe	Heavily grazed	Mixed grass	*Pheidole sp G*	1
			Pheidole sp G	1
			-	-
			-	-
			Monomorium sp A	1
			Pheidole sp T	1
			Pheidole sp G	2
			-	-
			-	-
			Monomorium sp A	2
			Pheidole sp G	2
			-	-
iMfolozi	Non- grazed	Mixed grass	-	-
			-	-
			Tetramorium constancia	1
			Monomorium delagoense	1

			Unknown	1
			Anoplolepis custodians	3
			Tetramorium constancia	1
			Anoplolepis custodians	32
			-	-
			-	-
			-	-
			Anoplolepis custodians	2
			-	-
iMfolozi	Lightly grazed	Mixed grass	*Monomorium delagoense*	12
			-	-
			-	-
			Monomorium delagoense	2
			-	-
			Anoplolepis custodians	10
			-	-
			-	-
			Monomorium delagoense	4
			-	-
iMfolozi	Heavily grazed	Mixed grass	*Monomorium delagoense*	7
			Anoplolepis custodians	1
			Monomorium delagoense	1
			-	-
			-	-
			Unknown	1
			Monomorium delagoense	1
			-	-
			-	-
			-	-
			-	-
			-	-
iMfolozi	Non-grazed	Tall grass	*Tetramorium sericeventre*	1
			-	-
			Monomorium sp D	1
			Pheidole sp A	1
			Pheidole sp G	3
			Monomorium delagoense	6
			Monomorium delagoense	3
			Pheidole sp G	3
			Pheidole sp B	1
			Monomorium sp A	1
			Monomorium delagoense	4
			Pheidole sp B	2
			Monomorium sp D	1
			-	-
			Monomorium delagoense	2
iMfolozi	Lightly grazed	Tall grass	*Monomorium delagoense*	1
			Monomorium delagoense	3
			Tetramorium sericeventre	3
			Monomorium delagoense	5
			-	-
			Monomorium delagoense	16
			Unknown	1
			Pheidole sp G	3
			Monomorium delagoense	5
			Tetramorium sericeventre	1
			Pheidole sp G	5
			Monomorium delagoense	26
			-	-
			Pheidole sp G	1

			Monomorium delagoense	12
			Pheidole sp G	1
iMfolozi	Heavily grazed	Tall grass	*Pheidole sp G*	2
			Pheidole sp G	3
			-	-
			-	-
			Monomorium delagoense	1
			Pheidole sp G	5
			-	-
			-	-
			Pheidole sp G	4
			-	-
			-	-
iMfolozi	Heavily grazed	Lawn	-	-
			-	-
			-	-
			-	-
			-	-
			-	-
			-	-
			-	-
			-	-
			Pheidole sp G	5

Appendix B: ANOSIM illustrating similarities between pairs of treatments in the Hluhluwe and iMfolozi sections in Hluhluwe-iMfolozi Park * denotes a significant difference.

	Test Statistic (R)	**Significance level (p)**
	0.338	**0.001**
Hluhluwe		
Tall none, Tall light	0.497	0.002*
Tall none, Tall heavy	0.012	0.450
Tall none, Mixed bunch none	0.048	0.267
Tall none, Mixed bunch light	0.196	0.052
Tall none, Mixed bunch heavy	0.175	0.050
Tall none, Lawn none	0.458	0.009
Tall none, Lawn light	0.478	0.002*
Tall none, Lawn heavy	0.533	0.001
Tall none, Mixed short none	0.425	0.002*
Tall none, Mixed short light	0.250	0.031
Tall none, Mixed short heavy	0.003	0.419
Tall light, Tall heavy	0.590	0.005
Tall light, Mixed bunch none	0.476	0.008
Tall light, Mixed bunch light	0.578	0.001
Tall light, Mixed bunch heavy	0.556	0.001
Tall light, Lawn none	0.364	0.034
Tall light, Lawn light	0.356	0.006
Tall light, Lawn heavy	0.282	0.005
Tall light, Mixed short none	0.593	0.002*
Tall light, Mixed short light	0.355	0.002*
Tall light, Mixed short heavy	0.549	0.002*
Tall heavy, Mixed bunch none	0.157	0.257
Tall heavy, Mixed bunch light	0.198	0.202
Tall heavy, Mixed bunch heavy	0.180	0.173
Tall heavy, Lawn none	0.648	0.029
Tall heavy, Lawn light	0.532	0.030
Tall heavy, Lawn heavy	0.582	0.009
Tall heavy, Mixed short none	0.556	0.024
Tall heavy, Mixed short light	0.201	0.131
Tall heavy, Mixed short heavy	0.074	0.286
Mixed bunch none, Mixed bunch light	-0.200	0.929
Mixed bunch none, Mixed bunch heavy	-0.165	0.870
Mixed bunch none, Lawn none	0.474	0.029
Mixed bunch none, Lawn light	0.357	0.034
Mixed bunch none, Lawn heavy	0.354	0.035
Mixed bunch none, Mixed short none	0.571	0.005
Mixed bunch none, Mixed short light	0.236	0.067
Mixed bunch none, Mixed short heavy	0.107	0.238
Mixed bunch light, Mixed bunch heavy	-0.132	0.948
Mixed bunch light, Lawn none	0.190	0.100
Mixed bunch light, Lawn light	0.216	0.033
Mixed bunch light, Lawn heavy	0.252	0.023
Mixed bunch light, Mixed short none	0.548	0.002*
Mixed bunch light, Mixed short light	0.383	0.009
Mixed bunch light, Mixed short heavy	0.248	0.037
Mixed bunch heavy, Lawn none	0.197	0.095
Mixed bunch heavy, Lawn light	0.215	0.017
Mixed bunch heavy, Lawn heavy	0.297	0.001
Mixed bunch heavy, Mixed short none	0.525	0.001

Mixed bunch heavy, Mixed short light	0.419	0.002*
Mixed bunch heavy, Mixed short heavy	0.279	0.017
Lawn none, Lawn light	-0.020	0.471
Lawn none, Lawn heavy	-0.087	0.670
Lawn none, Mixed short none	0.641	0.005
Lawn none, Mixed short light	0.413	0.014
Lawn none, Mixed short heavy	0.619	0.010
Lawn light, Lawn heavy	-0.053	0.757
Lawn light, Mixed short none	0.576	0.001
Lawn light, Mixed short light	0.453	0.001
Lawn light, Mixed short heavy	0.581	0.001
Lawn heavy, Mixed short none	0.615	0.002*
Lawn heavy, Mixed short light	0.471	0.001
Lawn heavy, Mixed short heavy	0.627	0.001
Mixed short none, Mixed short light	0.050	0.251
Mixed short none, Mixed short heavy	0.218	0.071
Mixed short light, Mixed short heavy	0.096	0.195
iMfolozi	**0.26**	**0.002***
Mixed bunch none, Mixed bunch light	0.245	0.114
Mixed bunch none, Mixed bunch heavy	0.407	0.086
Mixed bunch none, Tall none	0.336	0.018
Mixed bunch none, Tall light	0.708	0.004
Mixed bunch none, Tall heavy	0.823	0.029*
Mixed bunch none, Lawn heavy	0.667	0.200
Mixed bunch light, Mixed bunch heavy	-0.130	0.771
Mixed bunch light, Tall none	-0.057	0.597
Mixed bunch light, Tall light	-0.011	0.481
Mixed bunch light, Tall heavy	0.703	0.029*
Mixed bunch light, Lawn heavy	0.500	0.400
Mixed bunch heavy, Tall none	-0.119	0.725
Mixed bunch heavy, Tall light	0.055	0.370
Mixed bunch heavy, Tall heavy	0.944	0.029*
Mixed bunch heavy, Lawn heavy	1.000	0.250
Tall none, Tall light	0.039	0.230
Tall none, Tall heavy	0.209	0.088
Tall none, Lawn heavy	0.082	0.500
Tall light, Tall heavy	0.391	0.022
Tall light, Lawn heavy	0.420	0.222
Tall heavy, Lawn heavy	-0.333	0.800
Mixed bunch heavy, Tall none	-0.119	0.725

Appendix C: SIMPER showing ant species contributing to similarities between grazing level and grass type in Hluhluwe and iMfolozi sections in Hluhluwe-iMfolozi Park. * denotes species distinctive to a particular mixed grass type, ▪ denotes species distinctive to a particular grass type and grazing level.

Hluhluwe	**Average abundance (**number of ants/ per grass/per grazing level**)**	**Average Similarity**	**% contribution similarity**
Tall none			
Pheidole sp *G*	0.770	18.480	71.510
Myrmica natalensis▫	0.740	7.490	28.850
Tall light			
Anoplolepis custodians	1.770	35.550	100.00
Tall heavy			
Pheidole sp *A*▫	0.910	11.630	46.590
Pheidole sp *G*	1.000	13.330	53.510
Lawn none			
*Monomorium delagoense**	1.960	39.070	90.680
Lawn light			
*Monomorium delagoense**	1.000	37.500	88.420
Anoplolepis custodians	0.520	4.910	11.820
Lawn heavy			
*Monomorium delagoense**	1.290	27.410	71.460
Anoplolepis custodians	0.680	10.950	28.540
Mixed bunch none			
Pheidole sp *G*	0.750	23.030	61.230
Pheidole sp *S**	0.790	9.160	24.350
*Monomorium delagoense**	0.600	5.420	14.420
Mixed bunch light			
Pheidole sp *G*	0.690	7.260	23.840
Pheidole sp *S**	0.740	7.820	25.710
*Monomorium delagoense**	0.960	15.350	50.450
Mixed bunch heavy			
Pheidole sp *G*	0.440	7.240	22.090
Pheidole sp *S**	0.650	12.780	38.980
*Monomorium delagoense**	0.760	11.800	35.970
Mixed short none			
Monomorium sp *A*▫	1.080	38.630	100.000
Mixed short light			

Pheidole sp *P*▫	0.780	5.240	38.090
Monomorium sp *A*▫	0.860	8.520	61.910
Mixed short heavily			
Pheidole sp *G*	0.800	35.420	90.070
iMfolozi			
Tall none			
*Pheidole sp A**	0.290	1.330	7.340
Pheidole sp *G**	0.490	1.710	9.470
Monomorium delagoense	1.090	13.920	77.060
Tall light			
*Pheidole sp G**	0.750	5.710	13.380
Monomorium delagoense	2.470	36.140	84.750
Tall heavy			
Pheidole sp *G**	1.850	78.750	100.000
Mixed bunch none			
*Anoplolepis custodians**	2.200	24.920	81.080
*Tetramorium constancia**	0.500	5.820	18.920
Mixed bunch light			
Monomorium delagoense	1.720	35.670	100.000
Mixed bunch heavy			
Monomorium delagoense	1.550	48.380	100.000

CHAPTER 4

Concluding remarks

Ants are known to react rapidly to modifications in their habitat, with variation in their diversity, richness and abundance being regulated by richness of flora communities and microclimate. In this thesis, I used ants as indicator species to investigate the ecological effects of invasive plant invasions, grass types, grazing intensity and humidity in Hluhluwe iMfolozi Park (HiP), KwaZulu-Natal, South Africa.

In Chapter 2, I focused on understanding the changes in ant communities brought by *C. odorata* invasion over a short and long-term in HiP. From these results, it is evident that seasonal variation has a stronger influence on ant species distribution and community structure compared to invasions of *C. odorata*. I believe that this relatively minor effect of plant invasion is confirmed by an absence of specialist species in control and long cleared treatments, since communities consisting of generalists will have a higher likelihood to remain intact after disturbance. The absence of specialist native ant species combined with the high dominance of generalists and opportunist species in infested areas further supports this interpretation. However, it should also be noted that other environmental factors such as differences in soil type may have played a role in influencing ant distribution, and I suggest that these factors are included in future studies on the effects of plant invasions on invertebrate diversity.

The aim of Chapter 3 was to examine the effects of grazing intensity, grass height stature and grass type on ant communities in relation to variations in humidity within HiP. In this study, I found that humidity, grazing and grass type interacted in their effects on ant abundance, but that only humidity and grass type interacted in their effect on ant diversity. There was, however, an effect of grazing on ant diversity, but this effect was not altered by humidity or grass type. My result generally supported a higher abundance and diversity in the more humid Hluhluwe compared to the arid iMfolozi, which highlight the importance of humidity for ant communities. Moreover, the high ant diversity and species richness in lawn and mixed grass suggested that the heterogeneity within habitats is critical for long-term management of biodiversity. Finally, this study showed complex interactions between habitat, herbivory and climate variables in the effects on ant communities, and also that these interactions differed between effects on abundance versus effects on diversity.

To conclude, both my studies indicate a strong effect of climatic variables on ant community structure and abundance, either on seasonal (Chapter 2) or spatial (Chapter 3) scales, and such effects can both be stronger than the effects of plant invasions and considerably modify other environmental disturbances such as herbivory. Because of the suggested strong effects of climate on ant communities, I suggest that climate related disturbances, such as climate change, may have more severe impact on biodiversity than other anthropogenic perturbations. Mitigating climate effects of human disturbances should be prioritized in biodiversity conservation efforts.