Spider community responses to *Chromolaena odorata* invasion, grassland type and grazing intensities

By

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Declaration

I declare that the thesis hereby submitted in partial fulfilment of the requirements of the degree Magister Scientiae (Wildlife Management) at the University of Pretoria has not been submitted by me for any other degree at any other institution.

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Abstract

Biological indicators measure components of the biota and are used to give general information about complex ecosystems in which they occur, playing key roles in conservation planning and management. This study illustrates the impact of habitat change by factors that are extrinsic to the habitats in question and the importance of spider responses in aiding management decisions. The spider responses illustrated existence of environmental change and represent responses of other biota.

The conclusions drawn from this study have important management implications for protected areas with grazing herbivores and occurrence of alien invasive plants. Grazed sites showed the highest abundance, diversity and species richness, while ungrazed had the lowest. The implications from this study are that no grazing has negative

implications on lower trophic levels, whereas grazing seems to result in favourable conditions for optimal abundance, diversity and species richness.

The higher abundance, diversity and species richness associated with grazed sites could result from increased ground cover, greater variation in habitat structure, increased plant diversity and enhanced soil/plant nutrient concentrations. But, ungrazed sites in turn become more monotonous and provide less habitat diversity. However, the characteristic species for each grazing intensity level demonstrates the difficulty in making generalizations for management even for closely related species.

The results further opposed the assumption that grazing lawns are a result of overgrazing and thus highly undesirable. This grassland type in comparison to tall bunch grassland displayed the highest spider diversity and species richness. This evidence further supports the conclusion that grazing lawns are steady state communities of their own and not a sub-set of any other grassland type. Therefore, veld management decisions that eradicate grazing lawns are negative for the park as the fauna and flora associated with this grassland type will be lost, leading to cascading effects.

Additionally, this study illustrated that habitat modification by invasion of invasive alien plant species has detrimental consequences for the endemic fauna. *C. odorata* invasion results in a monotonous habitat structure. Consequently, structural heterogeneity is a primary determinant for spider diversity as opposed to abundance of prey, because plant height and architecture drive spider colonization.

Therefore, removal of alien invasive weeds results in returning a system to close approximation of its condition prior to disturbance with both structure and function recreated. Assemblage patterns can be selected as endpoints to measure the ecological rehabilitation; thus, the non-significant differences in assemblage patterns of the control *versus* cleared sites imply that the system is rehabilitating with clearing without further management intervention.

This study adds to the limited information on the implications of grazing intensities, grassland types, short and long-term invasion and clearing of an alien invasive plant on spider communities.

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“Worry does not empty today of its sorrow; it empties today of its strength.”

Unknown

CHAPTER 1

General introduction

Introduction

There are still some major gaps in our knowledge of biodiversity and one of these, typically, is that of the diversity of spiders in many areas (Dippenaar-Schoeman *et al.* 1989; Russell-Smith 2002; Whitmore *et al.* 2002; Warui, Villet & Young 2004; Dippenaar-Schoeman *et al.* 2005; Warui *et al.* 2005). Conservation biologists are now recognising the importance of the invertebrate component in the functioning of healthy ecosystems, but meaningful conservation cannot take place if the species involved are not known (Whitmore *et al*. 2002; Dippenaar-Schoeman *et al.* 2005).

Savannas are broadly defined to occupy more than twice the total area of rain forests, but very little attention has been paid to invertebrate diversity in savanna areas (Russell- Smith 2002). African savannas are distinct from other terrestrial ecosystems, because they have a high abundance and diversity of large herbivores. This study partly aimed at addressing this lack of knowledge on spider diversity in African savannas and was done in Hluhluwe-iMfolozi Park in northern KwaZulu-Natal, South Africa. A number of studies on invertebrates have been conducted in this Park, but not specifically on spiders (e.g. Rivers-Moore & Samways 1996; Samways & Kreuzinger 2001; Currie 2003).

SPIDER LIFESTYLE

Spiders are categorized according to their lifestyles or hunting habitats, i.e. wandering or the more sedentary spiders (web-builders) (Theodore & Savory 1928). Web-builders use their ability to produce silk for the construction of snares and they have developed quite different webs and prey-catching strategies, i.e. the orb-shaped web, funnel weavers, sheet-web weavers, cobweb tubular retreats (Theodore & Savory 1928), the scaffold-web, net throwing and finally kleptoparasites (live in webs of other spiders either feeding on prey remains in the web or preying on the host spider) (Filmer 1995).

Web-spiders are not randomly distributed in their environment and their population density is essentially limited by the availability of plant structures for web attachment (McNett & Rypstra 2000). Web-builders expend less energy in capturing prey as they sit and wait, while wandering spiders do not rely on a snare, but rather must overpower their prey directly. Wanderers could either be ground-dwellers (burrow-living and free-living spiders) or plant-dwellers (found in/living in grass, flowers, foliage and bark) (Filmer 1995).

Wanderers can further be divided into simple wandering spiders that pick up what is encountered or hunting spiders that overtake prey by speed, jump from a distance, lurk in concealment or seize the passers-by (Theodore & Savory 1928). Spiders have many foraging and habitat requirements that are reflected in taxonomic division of family, and families can be allocated based on known habitat requirements, e.g. moist habitat, generalists tolerant to dry habitats, disturbed open habitat specialists, and others (Harris, York & Beattie 2003).

FACTORS INFLUENCING SPIDER ECOLOGY

The distribution of spiders and their population density in habitats are functions of a whole range of graded factors within a given biotope. They are abundant in areas of rich vegetation but are also found in barren environments (Foelix 1982). Their abundance and distribution across habitats is influenced by temperature, humidity and many other abiotic factors (Duffey 1962; Foelix 1982; McNett & Rypstra 2000).

Low dispersal capabilities and high costs associated with web construction limit the web-spiders' ability to sample different localities (McNett & Rypstra 2000). Spiders tend to remain in selected sites and move only when the prey-capture is below some threshold, as they cannot move great distances and must thus remain in the same subhabitat (McNett & Rypstra 2000). A suitable microhabitat must satisfy a spider's particular physiological and web-construction requirements. It must provide a supply of prey and protection from predators. Spider population numbers are limited by the availability of suitable habitat structures, but it is unlikely that single factors operate alone to limit population densities (Riechert & Gillespie 1986).

A strong relationship between the spider and the habitat structure has been demonstrated by correlations and experimental manipulations (e.g. Balfour & Rypstra 1998; McNett & Rypstra 2000; Weeks & Holtzer 2000; Graham, Buddle & Spence 2003). For example, increasing the structural complexity of the habitat by intercropping, mulching, conservation tillage (Sunderland & Greenstone 1999) and higher weed densities (Balfour & Rypstra 1998) results in higher structural diversity and has been shown to enhance the density and diversity of spiders. There is a general agreement that structural diversity is important for invertebrate diversity (Mclyntyre 2005) and by definition, general carnivores that lack plant species requirements should be relatively more sensitive to plant architecture (Gibson *et al.* 1992a).

There are habitat differences in ground-dwelling spider communities that stem from fine scale differences in plant-cover types and height (Weeks & Holtzer 2000). Spider diversity is not correlated to prey availability, but to vegetation structure (Greenstone 1984). Vegetational complexity can be seen as an indicator of available microhabitat features, as well as abundance of potential predators and/or competitors in the habitat (McNett & Rypstra 2000). Density and patchiness of the vegetation understorey affects the temperature, humidity and light intensity at the ground level, and these factors influence spider habitat-selection and activity (Uetz 1991).

Vegetation structure plays an important role in providing web-attachment sites (Duffey 1962; Greenstone 1984; Janetos 1986; Rypstra 1986; Dippenaar-Schoeman *et al.* 2005) and in the composition of spider web-dwellers as it increases available retreat space (Dippenaar-Schoeman *et al.* 2005). Sites with tall composite plants for web attachment are predicted to provide the greatest probability for encountering and capturing prey (McNett & Rypstra 2000). The proportion of web-building spiders escalates with increasing vegetational complexity. The percentage cover of vegetation and variety in growth-forms determine the number of available websites (Janetos 1986).

The selection of a website is influenced by the habitat structure and microclimate, i.e. temperature, variations in humidity, light intensity, available points for web attachment and food supply (Duffey 1962). Web-spiders not only require habitats with specific microclimate, but also must meet certain spatial demands. For instance the environment must provide plenty of attachment sites for scaffolding of the web and sufficient open space (Greenstone 1984). All spider webs require physical support, and structural diversity of a habitat should be a good predictor of the diversity of web-spider species (Greenstone 1984).

SPIDERS AS BIOLOGICAL INDICATORS

A biological indicator is defined as a species that readily reflects aspects of the state of the environment within which it is found (McGeoch 2002). Indicators are important resource management tools (Lawes *et al*. 2005). Theodore & Savory (1928) noted that spiders are very sensitive to changes in the physical conditions of their environment. The simplicity of the spider’s assemblage response is advantageous for ecological studies, and it demonstrates their value as an indicator group for certain aspects for management effects (Gibson *et al*. 1992a). Spiders are generally accepted as indicator species (Gibson *et al*. 1992a; Gibson, Hambler & Brown 1992b; Martin & Major 2001; Niwa & Peck 2002; Scott, Oxford & Selden 2006). They are abundant, diverse and the more common species are easy to identify (Niwa & Peck 2002; Gibson *et al*. 1992a).

Spiders, as predators, occupy the top trophic levels and are likely to shape terrestrial arthropod communities (Martin & Major 2001). This means they are expected to integrate the biotic and abiotic influences affecting lower trophic levels (Scott, Oxford & Selden 2006). Generally it is agreed that an indicator group should: “(1) be large enough for responses to treatment; (2) depend on at least several species; (3) have an efficient sampling method; (4) be identified with ease, with respect to availability of literature, experts and the amount of work done for reliable identification; (5) show clear responses to management compared with temporal fluctuations, and (6) contain common species characteristics of all treatments applied and contain species characteristic of all stages. The single group that meets most of these criteria is spiders” (Gibson *et al*. 1992a). Reference is made to spiders, as they inhabit a large array of microhabitats and are thus suitable to integrate and evaluate activity by different guilds of herbivores (Foelix 1982). Also, a taxon’s actual performance as an indicator depends on its ability to reflect the responses of a wide range of ecosystem processes and components (Anderson 1999).

Forms of disturbance

Disturbance is any change to the properties of the ecosystem, such as structure, function or diversity, by factors that are extrinsic to the ecosystem under investigation (Abensperg-Traun *et al*. 1996). The current study focuses on the impact of mammalian grazing intensities and an invasive alien plant (*Chromolaena odorata* (L.) R.M. King and H. Robinson) on biodiversity using spider responses.

IMPACT OF GRAZERS ON SPIDER ECOLOGY

The extent to which changes in vegetation composition influence arthropod assemblages remains largely unknown (Seymour & Dean 1999; González-Megías, Gómez & Sànchez-Piñero 2004). Arthropods demonstrate a complex range of responses to environmental changes at both species- and community-level (Abensperg-Traun *et al*. 1996; Gibson *et al*. 1992a). Grazing has been found to have marked influence on the distribution of spider species and individuals (Duffey 1962; Gibson *et al*. 1992a; Gibson, Hambler & Brown 1992b; Abensperg-Traun *et al*. 1996; González-Megías, Gómez & Sànchez-Piñero 2004; Cingolani, Posse & Collantes 2005; Warui *et al*. 2005). It has been demonstrated that larger web-spinning species are more sensitive to grazing pressure (Gibson, Hambler & Brown 1992b; Dennis 2003).

The impact of grazers has been demonstrated to be negative, positive or neutral. **Negative**: the total abundance is illustrated to decrease with grazing (Morris 1968; Gibson, Hambler & Brown 1992b; Warui *et al*. 2005) and there is a reduction in faunal composition (Gibson, Hambler & Brown 1992b). **Positive**: significant increase in arthropod abundance with increasing disturbance and the greatest abundance under moderate disturbance (Abensperg-Traun *et al*. 1996). González-Megías, Gómez &

Sànchez-Piñero (2004) illustrated a general negative response of arthropods, to the exclusion of ungulates, as there was lower diversity and biomass in ungrazed plots. Heavy grazing seems to prevent fast successional change in the fauna, while also allowing the possibility for other more rare species to become established, as demonstrated by Gibson *et al.* (1992a) and Warui *et al*. (2005). **Neutral**: Harris, York & Beattie (2003) demonstrated no significant difference between grazed and ungrazed sites.

Hluhluwe-iMfolozi Park is home to a number of indigenous ungulate species. Faunal exclusion plots were employed in this study to compare abundance, species compositional structure and diversity of spider communities along an increasing grazing-intensity gradient, in four different grass types (tall bunch grass, grazing lawns, herb and mixed grass). Grazing lawns are often perceived to be overgrazed by rangeland scientists and it has been thought that they should be eliminated by managing grazer assemblages, but they could be important contributors to savanna biodiversity. If there is a specific spider assemblage owing to this grassland type that will imply that it is a stable state community on its own (Bond, pers. comm.). The study area further offered comparison in spider assemblage patterns due to altitudinal and rainfall gradients. The key questions are:

(1) What is the impact of a grazing intensity gradient on spider abundance, diversity, and species richness?

(2) Are the spider communities on grazing lawns a subset of those in tall bunch grass grasslands?

(3) What is the effect of variations in rainfall and altitudinal gradients on spider assemblage patterns?

Rationale

Very little direct investigation of the effects of grazing on biodiversity has occurred in South Africa or elsewhere. Heavily grazed areas can be a resource for vertebrate herbivores, which can benefit from the high quality forage associated with grazing lawns (Mclyntyre 2005), but the implications are not completely known on the invertebrate community. There also have not been many detailed studies on spiders that have focused on the relationship between species richness and altitude (Chatzaki *et al*. 2005). We, therefore, need to understand the impacts of habitat change on local fauna. Also, conservation cannot be fully effective if the species to be conserved are unknown. Results from this study have important management implications for managing grazer assemblages, as the impacts for different grazing intensity levels have been determined and these results have practical implications for grazer stocking levels.

IMPACT OF INVASIVES

Invasive species are defined as non-native organisms that cause, or have potential to cause, harm to the environment (Sharma, Singh & Raghubanshi 2005). Exotic species invasion is amongst the most important problems experienced on a global scale by natural ecosystems (Sharma, Singh & Raghubanshi 2005). There is an increasing realization of the ecological costs of biological invasion (Sharma, Singh & Raghubanshi 2005). Natural environments are increasingly disappearing and degrading, and this has generated a need to conserve and restore biological diversity (Gratton & Denno 2005).

Biological invasions alter ecosystem processes in invaded areas, thus causing functional and compositional change (D’Antonio & Vitousek 1992). Invasions that alter the functioning of the ecosystem represent a significant threat to native populations and communities, as they don’t merely compete with or consume native species, but also change the ecosystem dynamics by altering environmental conditions or resource availability (D'Antonio & Vitousek 1992). Invasive alien plants can negatively affect all components of biodiversity from genes to ecosystem processes (Higgins *et al*. 1999).

Thus, several measures have been developed and deployed to control, contain or eradicate a wide range of invasive species in affected areas. Invasive alien plants erode natural capital, compromise ecosystem stability and threaten economic productivity (Richardson & van Wilgen 2004). South Africa has a long-standing history of problems with invasive alien species, research and management of biological invasions (Macdonald 2004; Richardson & van Wilgen 2004).

Invasive plant species can be considered as "ecological engineers" as they modify the ground surface microenvironment. Arthropods are closely associated with native vegetation or the microhabitats created, and a decrease in the dominant plant species and alteration of the physical characteristics of a habitat are generally expected to have negative consequences for the native fauna (Gratton & Denno 2005). Progressive invasion by an invasive alien plant alters the composition of plant species and the physical structure of the habitat, and radically changes arthropod assemblages in native habitats (Gratton & Denno 2005).

The extent to which the native invertebrate community is restructured may vary with the degree of the change to the vegetation structure (Harris *et al.* 2004). The replacement of native plant species could indirectly reduce the abundance and diversity of terrestrial arthropods. This could decrease resources for higher-order terrestrial consumers and alter terrestrial inputs (Greenwood, O'Dowd & Lake 2004). Dominance of an ecosystem by exotic plant species will not necessarily result in the reduction of species diversity (Harris *et al.* 2004). The impact of invasives has been demonstrated to be positive, negative and neutral.

Positive: Pétillon *et al*. (2005) illustrated that species and taxonomic richness were higher in invaded stations compared to associated natural ones. Harris *et al.* 2004 found many native invertebrate species that were unique in both the native and invaded habitat. The invaded habitat contained at least as many or more native species than the native habitat in all insect groups, which indicates that the invaded habitat has value as a habitat for native invertebrates.

Negative: Greenwood, O'Dowd & Lake (2004) illustrated that native areas had a significantly greater diversity of terrestrial species compared to invaded areas. Samways & Taylor (2004) reported on the threats to Odonata, especially by invasive alien trees, and predicted that removal of these invasives is likely to increase the long-term survival of these species. Samways, Taylor & Tarboton (2005) later found three species of Odonata that appeared only after the invasive alien trees had been removed and the natural vegetation had been re-established. Successful eradications often lead to dramatic recovery of native species and ecosystems (Zavaleta, Hobbs & Mooney 2001). Watts & Gibbs (2000) studied restored areas after alien plant removal and found that the re-establishment of indigenous beetle species was promoted, although it can take a long time. Gratton & Denno (2005) demonstrated that the removal of an invasive alien plant resulted in the restoration of the arthropod assemblage associated with the native habitat.

Neutral: Sax (2002) found that species richness was nearly identical in the native and the invaded habitat, but the compositions were different. This study highlights that ecosystem dominance by an exotic plant species will not necessarily result in the reduction of species diversity.

BACKGROUND INFORMATION ON *Chromolaena odorata*

Chromolaena odorata is commonly known as 'triffid weed', 'eupatorium' or 'isandanezwe' in South Africa (Macdonald 1983). Elsewhere it is also known as the Siam weed and was formerly known as *Eupatorium odoratum* (Apori *et al.* 2000). *C. odorata* is a perennial hexaploid weed, which flourishes in humid, open forest areas (Ambika 2002). Its distribution is limited to warm and humid tropical regions, latitudes of about 30°N and S, and an altitude of about 1000m near the equator. This weed thrives in regions with rainfall of 200cm and above per annum, and a temperature range of 20° to 37°C (Ambika & Jayachandra 1990). *C. odorata* is native to the neotropics from Eastern USA, Central America and most West Indian Islands.

C. odorata was first recorded in Hluhluwe-iMfolozi Park in 1961, where its population was beginning the "exponential phase" of its population increase in the reserve (Macdonald 1983). It is the most widespread invader in Hluhluwe-iMfolozi Park (Macdonald 1983; Howison & Balfour 2002). Its distribution was first mapped in the Hluhluwe-iMfolozi Park in 1983 and indicated 50ha of infestations in the 13 points at which the species was recorded (Macdonald 1983). In 1998 it was re-mapped, and this study revealed dense infestations of approximately 2 100ha (Howison & Balfour 2002). Further work was done in 2001 and revealed 5 600ha of infestation.

Nearly all the protected areas in KwaZulu-Natal have already been invaded by this weed (Macdonald 1983). It is a major tropical weed worldwide and the most problematic non-native invasive plant species in the KwaZulu-Natal province of South Africa. Robertson *et al.* (2003) ranked *C. odorata* as the weed species in South Africa that is the second greatest problem and requires present and future management action, Lantana (*Lantana camara* L.) being the first most problematic. Macdonald (1983), in comparison, ranked it as the alien invader posing the greatest threat to the natural vegetation in the Hluhluwe-iMfolozi Park, as it suppresses the natural vegetation and reduces the diversity of species.

C. odorata is capable of extremely rapid growth to form impenetrable tangles, which eventually shade out all the indigenous vegetation. It reduces the grassland, savanna and forest vegetations to monotypic vegetation irrespective of the systems properties (Goodall & Zachariades 2002). Its worst attribute is that it is highly flammable and even burns when green in midsummer (Macdonald 1983). The increased fuel load causes seasonal fires to burn with greater intensity in invaded ecotones, resulting in damage to the indigenous vegetation (Zachariades & Goodall 2002). To date, *C. odorata* is not under successful biological control in South Africa (Strathie & Zachariades 2002).

Thus, this study will determine the affects of *C. odorata* invasion durations and clearing on invertebrate communities, employing spider responses. The key questions are: 1) Do *C. odorata* invasions alter native spider assemblage patterns? 2) Do different invasion durations of *C. odorata* have a varying effect on native spider assemblage patterns? And lastly, 3) do native spider assemblages re-establish after *C. odorata* clearing without further management intervention?

Rationale

Exotic plant species change the structure of a habitat and invertebrates are sensitive to changes in habitat structure. There are a number of reasons to suspect that alien plants negatively affect native invertebrates, as at least 90% of all phytophagous insects are specialists and have evolved in concert with only one or a few plant lineages (Tallamy 2004). Of particular concern is the invasion of alien plants into unspoiled ecosystems, since these systems are important stores of biodiversity (Higgins *et al*. 1999).

The grassland and savanna biomes have been extensively invaded in South Africa and one of the important species here is *C. odorata* (Richardson & van Wilgen 2004). The objective of the Hluhluwe-iMfolozi Park is to maintain viable populations of as many indigenous species in the reserve as possible, and this objective can only be achieved if invasion in this area is controlled (Macdonald 1983). The introduction of non-indigenous species is a direct threat to the whole of the reserve, which is protected for its unique biota (Blossey 1996).

It is fundamental to our understanding of invasive species management that the impact that they have on native communities is documented and that it is determined whether native communities can be restored following removal of invasives (Gratton & Denno 2005). Thorough understanding is necessary for the development of basic ecological principles for managing these invasions (D'Antonio & Vitousek 1992).

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CHAPTER 2

Spider responses to mammalian herbivore grazing: the effects of grazing intensity, rainfall, altitude and grassland type.

Abstract

1. Grassland structure and composition are modified by mammal herbivore grazers. Heavy grazing of tussock/bunch grassland results in a compositional shift of grass species to form grazing lawns. The impacts of these changes on other grassland biota are not well documented in African savannas. Grazing lawns have always been thought to be an undesirable outcome of over grazing. However, they could be their own stable state grassland community and thus important and significant contributors to savanna biodiversity. Therefore, a better understanding of structural change is needed in order for management to maintain and maximise diversity.

2. Spiders are excellent ecological indicators as they integrate activity by different guilds of herbivores and have simple responses. Pitfall traps and sweep netting were used to sample spiders in Hluhluwe-iMfolozi Park in September 2005 along 1) a grazing intensity gradient, 2) grazing lawns *versus* tall bunch grasses and 3) rainfall and altitude gradients.

3. Higher species richness was observed in moderately and intensely grazed sites in comparison to ungrazed sites for both pitfall trap and sweep net data. No significant differences were observed between moderately grazed and intensely grazed sites and this may be a consequence of structural heterogeneity.

4. A distinct spider assemblage pattern on grazing lawns was observed, indicating that grazing lawns are not just depauperate tall-grass systems. On the contrary, higher abundance, diversity and species richness of spiders was observed on grazing lawns than in tall, bunch grassland.

5. Sites of different rainfall and altitudes had distinct spider assemblages.

6. *Synthesis and applications*. Diversity is higher in grazed sites. As a consequence of no grazing due to under stocking mammalian herbivores, biodiversity is negatively impacted upon. Grazing lawns are stable state communities supporting flora and fauna specialists that prefer this grass type. Loss of grazing lawns may have cascading effects, therefore management decisions with regards to fire regimes and management of grazer assemblages should make considerations for promoting and/or maintaining grazing lawns, as the presence of all grass types is considered optimal for conserving biodiversity.

Key-words: African savanna, compositional structure, exclosure, grazing lawn, Hluhluwe-iMfolozi Park, Intermediate Disturbance Hypothesis, pitfall traps, species richness, sweep netting, tall bunch grass

Introduction

Large herbivores, which are characteristic of African savannas, affect grassland community composition and structure through their grazing (Augustine & McNaughton 1998). Heavy utilisation of tall bunch grasses by herbivores can lead to the development of grazing lawns as tall bunch grasses are eliminated and replaced by small tufted and/or creeping grasses and forbs, which are more tolerant of grazing (Krook 2005; Mclyntre 2005; Waldram 2005).

Rangeland scientists have often perceived these grazing lawns to be over-grazed, and most rangeland management involves manipulating grazer numbers and distributions to prevent grazing lawn establishment. However, grazing lawns are persistent features of many natural grazing systems (Bond, pers. comm.). They are therefore increasingly being recognised as an essential component of natural grazing ecosystems. Less is known about the bird, mammal, and insect fauna associated with these grazing lawns.

The extent of grazing lawns in a system appears to be quite variable – depending on factors such as grazer density, fire frequency, and rainfall (Archibald *et al.* 2005). For managers to decide how important it is to conserve and manage for grazing lawn systems, they need to have information on the biodiversity associated with these grass communities.

Krook (2005) found that grazing lawns are both structurally and floristically different to tall bunch grassland, and support high densities and diversity of grazing herbivores. Grazing lawns could therefore be important contributors to biodiversity, and some studies have found unique biotic assemblages on these short-grass communities (i.e. Currie 2003; Skowno & Bond 2003, Krook 2005; Waldram 2005, etc.). However, no one has yet looked at arthropod assemblages.

Thus, questions have recently been raised regarding the sustainability of these grazing lawns (Currie 2003; Krook 2005; Waldram 2005). If there is a specific assemblage owing to this grassland type that is not a subset of any other grassland type, then that implies that grazing lawns are stable state communities on their own. This then poses a further question: have we inherited a legacy, a grassland type that is distinctly African (Bond, pers. comm.)?

Plant structural diversity is important for the composition and diversity of invertebrate assemblages (Gibson *et al.* 1992a; Mclyntyre 2005). Natural underlying patterns of environmental variability have been shown to affect invertebrate assemblage patterns and invertebrate faunas vary distinctly with management regimes (Woinarski *et al.* 2002). Disturbances such as grazing have been shown to modify invertebrate successional assemblage patterns (Gibson *et al.* 1992a). Spiders are considered an excellent indicator group (Gibson *et al*. 1992a; Gibson, Hambler & Brown 1992b; Martin & Major 2001; Niwa & Peck 2002; Scott, Oxford & Selden 2006) and are useful for ecological studies due to their simple responses to management effects (Gibson, Hambler & Brown 1992b). They also inhabit a large range of microhabitats making them suitable to integrate and evaluate activity by different guilds of herbivores (Foelix 1982). Moreover, it has been shown that grazing has a marked influence on the distribution of spider species individuals (Duffey 1962; Gibson *et al.* 1992a; Gibson, Hambler & Brown 1992b; Abensperg-Traun *et al*. 1996; González-Megías, Gómez & Sànchez-Piñero 2004; Cingolani, Posse & Collantes 2005; Warui *et al*. 2005).

Species richness or diversity is one of the most simple and understandable concepts for characterizing community diversity. It is important for comparing communities in conservation and management of biodiversity and it is employed to assess effects of disturbances and for making environmental policy decisions. In light of the above, this study aims to assess the impacts of herbivore grazing on biodiversity using spider responses. The three key questions posed this study are:

(1) What is the impact of a grazing intensity gradient on spider abundance, diversity, and species richness?

(2) Are the spider communities on grazing lawns a subset of those in tall bunch grass grasslands?

(3) What is the effect of variations in rainfall and altitudinal gradients on spider assemblage patterns?

Results from this study will promote a better understanding of the impacts of grazing on biodiversity, and will contribute to the knowledge of South African spider species.

Materials and methods

STUDY AREA

Hluhluwe-iMfolozi Park (HiP), is situated between the latitudes 28°00' and 28°26'S and longitudes 31°43' and 32°09' E, in KwaZulu-Natal, South Africa. It encompasses 900 km^2 and is comprised of a northern section (Hluhluwe, 300 km^2) and a southern section (iMfolozi and corridor, 600 km^2) (Kruger, Lawes & Maddock 1999). The topography is hilly with an altitude range from 60 to 540 m a.s.l. (Kruger, Lawes & Maddock 1999). HiP has unimodal rainfall (Macdonald 1983) with a mean annual rainfall of 990 mm in Hluhluwe and 720 mm in iMfolozi (Whateley & Porter 1983). The park is a complex mixture of vegetation types: open grasslands, savannas and thick bush. It appears that in the early 1960's grazing lawns were more extensive in Hluhluwe-iMfolozi Park, but have now shifted to tall bunch grassland (Waldram 2005). The environment and vegetation of the reserve are described by Whateley & Porter (1983). Amongst its fauna HiP is home to a number of indigenous mammal herbivore grazers such as: white rhinoceros *Ceratotherium simum* (Burchell), African elephant *Loxodonta africana* (Burchell), warthog *Phacochoerus africanus* (Pallas), impala *Aepyceros melampus* (Lichtenstein), black rhinoceros *Diceros bicornis* (Linnaeus), blue wildebeest *Connochaetes taurinus* (Burchell) and Burchell's zebra *Equus burchelli* (Gray).

EXPERIMENTAL DESIGN AND SAMPLING METHODS

We used 10 grassland exclosure plots in HiP, five in Hluhluwe and five in iMfolozi Hluhluwe represents a high rainfall/altitude site, and iMfolozi a low rainfall/altitude site. Each exclosure plot contained three 40 m x 40 m sites (n = 30 for HiP) that exclude different grazing mammals by means of a fence. They are as follows: 1) intense grazing – unfenced and all animals present, 2) moderate grazing – partial exclosure, excluding larger grazers i.e. white rhinoceros *Ceratotherium simum* and African elephant *Loxodonta africana*, and 3) no grazing – all animals down to the size of a scrub hare *Lepus saxatilis* excluded. Each exclosure plot in Hluhluwe is located in one of the following five grassland types: mixed grass (lawn/tuft but mostly short grass), mixed grass (lawn/tuft but mostly bunch grass), tall bunch grass, grazing lawn, and herb. The same holds true for the plots in iMfolozi. For the purpose of answering whether grazing lawns are their own stable state communities and not a subset of tall bunch grasses, only comparison between the tall bunch grassland and the grazing lawns was made. Waldram (2005) found that grazing lawns are predominately dominated by members of the grass sub-tribe Chloridoidea with mostly *Urochloa mosambicensis* (B.); *Dactyloctenium australe* (W.) and *Digitaria longiflora* (H.), while tall bunch grasses are members of the sub-tribe Andropogonae, with mostly *Themeda triandra* (F.), *Heteropogon contortus* (P.) and various species of *Hyparrehenia* (F.), *Bothriocloa* (K.) and *Cymbopogon* (S.).

More detailed differences between grazing lawns and bunch grasses are described by Archibald *et al.* (2005), and further descriptions on grazing lawns are outlined by McNaughton (1984). The location and set-up of the exclosure plots also allowed for comparing the impacts of rainfall and altitude between the sites in the Hluhluwe section and the iMfolozi section of HiP. The spider sampling was done in September 2005 (spring). The limitations of invertebrate sampling are widely recognized. Certain species may dominate at certain times of the year (Whitmore *et al*. 2002) and this study is essentially a ‘snapshot’ in time as the data were collected in early spring only. However, in comparative studies where impact disturbance is being investigated, ‘snapshot” studies are a serviceable tool provided the timing is taken into account (Sørensen *et al.* 2002). We used pitfall traps and sweep netting because mechanical methods such as these are less subject to human bias (Sørensen *et al.* 2002).

Pitfall traps

Pitfall traps were employed because they are widely used and efficiently capture spiders (including larger species) and give good estimates of mobility when employed with other sampling methods (Gibson, Hambler & Brown 1992b). However, they are prone to damage by large animals. In anticipation of some animal damage a high a number of these traps was employed. Within each of the 30 sites, 10 pitfall traps were set up in a rectangular grid (2 m x 8 m) with 2 m spacing between traps (n = 300 traps for HiP). Small smooth-sided plastic vials (3.5 cm across and 13.0 cm deep) were sunk into the ground so that the lip of the vial was flush with the ground surface (Gibb & Hochuli 2002; Sørensen *et al.* 2002; Witt & Samways 2004). The vials were left open in the ground and filled with approximately 2 cm, 50/50 mixture of water/propylene glycol and a few drops of liquid soap. The traps were left out for 72 hours after which they were collected. After collection the spiders were separated from other invertebrates and stored in vials containing 70% ethanol (Sunderland *et al.* 1986; Green 1999; Henaut 2000; Russell-Smith 2002). The spiders were identified to morphospecies and species level by a specialist at the Agricultural Research Council in Pretoria.

Sweep netting

Sweep netting was employed to access ground level and low vegetation fauna and to give good estimates of spider abundance (Sørensen *et al.* 2002). Within each of the 30 sites, a 55 cm diameter sweep net was swept randomly for three full lengthwise laps in the 40 x 40 m sites. The same person sampled all sites. The net was emptied on regular intervals to avoid loss and destruction of the specimens. The specimens were killed by refrigeration at approximately 3°C to avoid loss when separating the specimens from any plant material collected while sweep netting, and then stored in 70% ethanol.

DATA ANALYSIS

Diversity indices

To describe the pattern of spider abundance for the different grazing intensity levels, grass types and areas varying in altitude and rainfall, three most widely used species diversity measurements in ecological studies were calculated: Simpson's index (1-λ), Shannon-Weiner (H'), Margalef (d) and total species richness using the PRIMER software programme (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick 2001). Kolomorgov-Smirnov one-sample test (test for normality) (*H*) was computed using SigmaStat 3 software package (www.sigmastat.com).

Non-parametric methods were used to compare abundance, diversity, species richness and guild structures along a grazing intensity gradient, grass types and areas of varying altitude and rainfall. The Mann-Whitney U (*U*) and Kruskral-Wallis (*H*) tests were applied to the data using the software package STATISTICA 6 (http://www.statsoft.com). As spiders occupy defined environments and have limitations set by physical conditions and biological factors (Foelix 1982), their species can be grouped into guilds based on the available information on their preferred habitats and predatory strategies (Dippenaar-Schoeman *et al.* 2005). Therefore, the spiders were allocated to their guilds primarily using Dippenaar-Schoeman *et al.* (2005) and secondarily Dippenaar-Schoeman & Jocquè (1997). The guilds they were allocated to were: orb web, space web, scaffold web, gum-foot web, free ground dweller, free plant dwellers, free plant wanderer and burrowing ground dweller.

Similarity analysis

The extent of association or similarity between sampling methods and between areas varying in rainfall and altitude was investigated employing ordination techniques. Non-metric Multidimensional Scaling (nMDS) analyses on the PRIMER 5 were computed to determine spider assemblage changes. This method is considered the preferred method of ordination technique for assemblage data (Clarke & Warwick 2001). Additionally, Analyses of Similarity (ANOSIM; *R*) were used to establish if there were significant differences in spider assemblages in areas of varying rainfall and altitudinal gradients, and Similarity percentages (SIMPER) routines were used to identify the spider species that contributed to the observed patterns. Geometric class plots were employed to illustrate differences in spider species classes between different grassland types.

Estimated species richness

Species accumulation curves based on spider catch data were plotted in order to assess sampling adequacy and completeness of the inventory (Coddington, Young & Young 1996). Single observed species (SOBs) were identified employing EstimateS 7 software package (http://viceroy.eeb.uconn.edu/estimates). Samples were randomly selected without replacement and SOBs represented cumulative numbers of species. Invertebrates are nearly impossible to sample exhaustively, and in such cases, non-parametric estimators are used to compensate for the non-exhaustive sampling adequacy (Gotelli & Colwell 2001). Thus, Chao second order (Chao 2) and Jackknife second order (Jack 2) species richness estimators were computed using the EstimateS 7 software package since they provide the least biased estimates of species richness for small numbers of samples (Colwell & Coddington 1994).

Results

A total of 563 spiders, from 79 species and 25 families, were captured. Of these, 163 individuals from 35 species in 18 families were caught in the pitfall traps and 405 individuals from 52 species in 21 families retrieved from sweep netting. The spider assemblages found in pitfall traps and sweep netting were significantly different (Figure 1, *R* = 0.542, *P* = 0.001), and were therefore analysed separately. The species accumulation curve indicated good sampling adequacy (Fig. 2). The spider species accumulation curves were asymptotic, with number of new species caught levelling off above 20 samples (Fig. 2). This indicates that the sampling replication used (10 per site) was adequate.

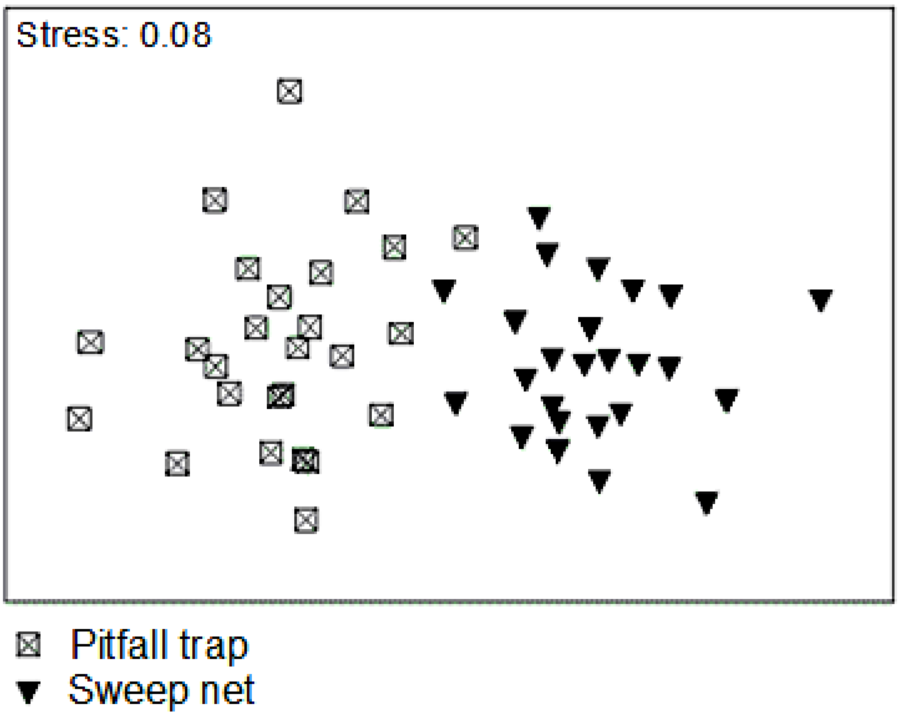

Fig. 1. The two sampling methods employed in this study (pitfall trap and sweep net) at species level clustered into two separate groups (Non-metric Multidimensional Scaling on Bray-Curtis similarities, stress 0.08). Theses differences were significant (ANOSIM *R* = 0.542, *P* = 0.001).

GRAZING INTENSITIES

Higher spider species diversity was found in both intensely and moderately grazed sites with the ungrazed sites consistently lower (Table 1). The ungrazed sites illustrated the lowest diversity for Margalef's index, Shannon-Wiener index, Simpson's index and observed species richness for pitfall trap data.

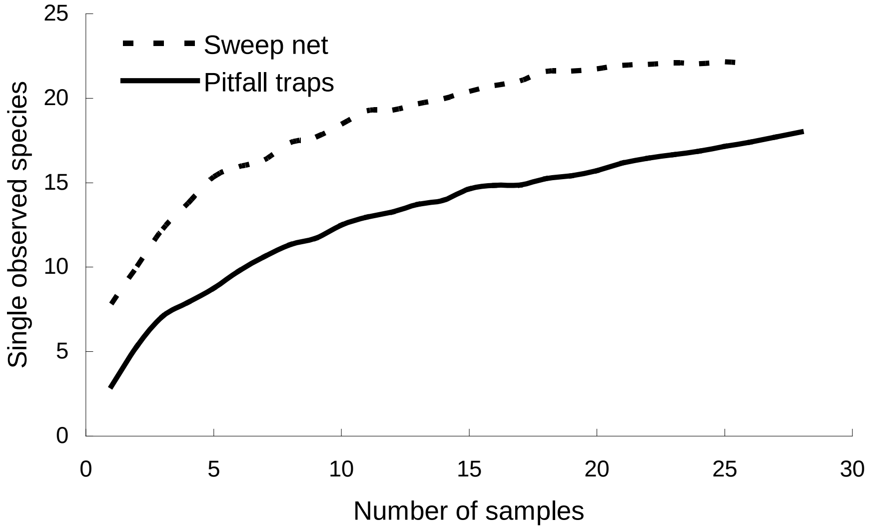

Fig. 2. Spider species accumulation curves for pitfall trapping and sweep netting in HiP during September 2005.

This trend further proved to be significant for estimated species richness for pitfall trap data (Fig. 3a; $F_{2,27} = 5.765$, $P < 0.01$) and the sweep net data (Fig 3b; $F_{2,25} = 13.83$, $P < 0.01$). No significant differences were observed between intensely and moderately grazed sites for both pitfall trap and sweep net data. SIMPER routine showed species that were characteristic of each grazing level (Table 2) and illustrated that moderately grazed sites were characterized by the highest number of species.

The ungrazed sites had the highest number of unique species (Table 3). At a family level, intensely grazed levels were dominated by Philodromidae (21%, six species), Pisauridae (20.6%, two species) and Salticidae (15.6%, six species); moderately grazed levels were dominated by Thomisidae (19.6%, nine species), Pisauridae (19.2%, two

Table 1. Mean spider diversity indices for pitfall trap (PT) and sweep net (SN) sampling under each grazing intensity level studied in HiP during September 2005. Showing the highest abundance and observed species richness for the moderately grazed sites for both PT and SN.

Diversity Index	**Intense grazing**		**Moderate grazing**		**No grazing**		**Bunch grass**		**Grazing lawn**	
	PT	SN	PT	SN	PT	SN	PT	SN	PT	SN
N	5.2	14	7.0	19	5.1	15	4.6	13.8	8	11.5
S	3.4	4.9	3.6	7.8	3.1	7.6	3.2	4.8	4.7	6.8
D	1.6	1.6	1.5	2.3	1.3	2.4	1.5	1.5	1.9	2.3
H'(loge)	1.0	1.1	1.0	1.5	0.8	1.6	1.1	1.2	2	1.4
1-Lambda	0.56	0.58	0.59	0.69	0.48	0.70	0.62	0.66	0.69	0.65

N = mean abundance; S = mean observed species richness; d = mean Margalef's;
H' log e = mean Shannon-Wiener; 1-Lambda = mean Simpson's

species) and Ammoxenidae (13.2%, three species); and intensely grazed sites were dominated by Pisauridae (20.0%, one species); Thomisidae (15.9 %, nine species) and Oxyopidae (13.1%, one species) (Appendix A).

GRASS TYPES

Grazing lawns displayed the highest spider diversity (Margalef's and Shannon-Wiener index) and observed species richness (Table 1). Furthermore, SIMPER illustrated that grazing lawns had a higher number of uniquely characteristic species that were not shared with bunch-grass communities (Table 4). SIMPER recognised seven unique species as contributors to the characteristic species of grazing lawns with only two species recognised as uniquely characteristic for the tall bunch grass.

The geometric class plot for pitfall trap (PT) data further illustrated the different spider compositional assemblage structures of grazing lawns and bunch grasses (Fig. 4). Grazing lawns have a higher percentage of unique species as the percentage of spider species in the geometric class of 1 (species that only occur once) is over 60%, while for bunch grass it is over

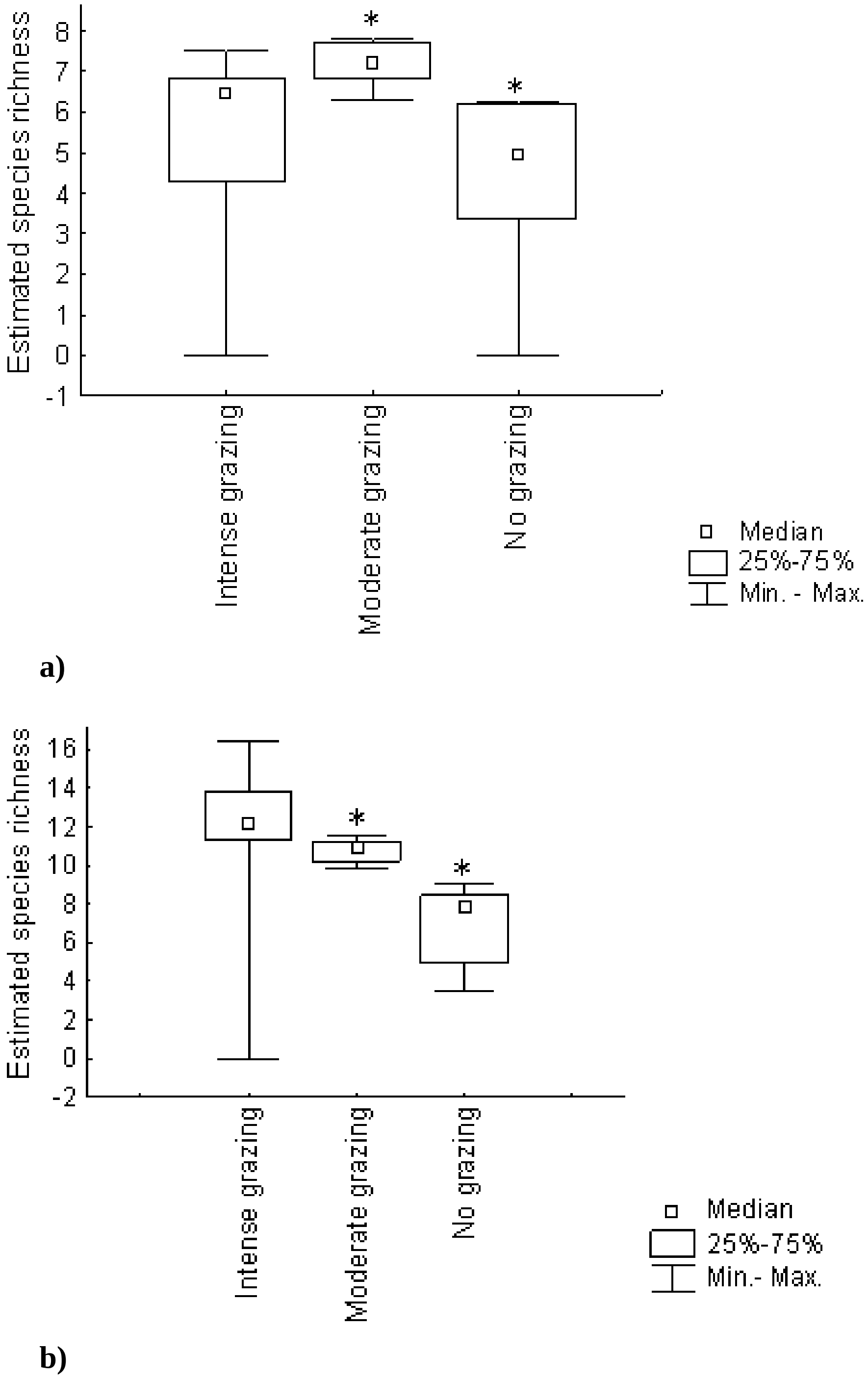

Fig. 3. Estimated spider species richness for different grazing intensity levels a) pitfall trap data showed significant differences between moderately grazed and ungrazed sites ($F_{2,27} = 5.765$, $P < 0.01$) and b) sweep net data illustrated significant differences between moderately grazed sites and ungrazed sites ($F_{2,25} = 13.83$, $P = 0.01$). Asterisks indicate grazing intensities for which there were significant differences in estimated spider species richness ($*P \leq 0.001$). Bars indicate 25-75%.

only 40%. Furthermore, this plot illustrates that the plot for grazing lawns extends over more class ranges, while the bunch grasses have species in fewer class ranges and a lower number of unique species. Thirty species were unique to the grazing lawns and only nine were unique to the tall bunch grass (Table 5 and Appendix B). The dominant families on grazing lawns were Thomisidae (25.0%, eight species), Salticidae (14.4%, seven species) and Ammoxenidae (13.4%, one species); and the tall bunch grass was dominated by Pisauridae (42.3%, three species), Philodromidae (20.5%, five species) and Salticidae (19.2%, two species).

VARIATIONS IN ALTITUDE AND RAINFALL

The nMDS for areas varying in altitude and rainfall clustered into separate groups demonstrating different assemblage structures (Fig. 5, $R = 0.493$, $P = 0.001$). The two different sections had similar numbers of species (Appendix C) and similar numbers of unique species (Hluhluwe had 27 unique species and iMfolozi 25 (Appendix C).

Hluhluwe was dominated by Thomisidae (25.0%, eight species), Araneidae (9.4%, eight species) and Salticidae (11.3%, six species), while iMfolozi was dominated by Pisauridae (24.0%, two species), Ammoxenidae (14.0%, one species) and Salticidae (14.0%, seven species). More than double the number of specimens was captured in iMfolozi in total (409) in comparison to the number captured in Hluhluwe (158) (Appendix C).

Table 2. SIMPER routine from pitfall trap (PT) and sweep net (SN) data, illustrating spider species that are characteristic and contribute to the overall similarities for each grazing intensity level, average abundance of each species in each grazing level, similarity observed within the grazing level and the percentage contributed by each species to the similarity of a given grazing level. Symbols: * denotes species characteristic to intense and ungrazed sites, ‡ characteristic to moderate and ungrazed sites, † uniquely characteristic to each grazing level and ** to all three grazing levels.

Spider species per grazing intensity level	**Average abundance of total**		**Average similarity of total**		**% contribution to similarity among grazing level**	
	PT	SN	PT	SN	PT	SN
Intense grazing						
Aelurillus sp 1*	-	0.25	-	1.02	-	10.63
*Afropisaura rothiformis***	-	3.63	-	5.09	-	53.02
*Aphantaulax inornata**	0.50	0.50	-	0.70	-	7.30
Camillina sp 1†	0.33	-	1.94	-	14.89	-
Cydrela sp 1**	0.22	-	1.39	-	10.63	-
Monaeses quadrituberculatus	-	0.83	-	1.22	-	12.71
Oxyopes sp 1†	-	2.38	-	1.09	-	11.34
Pardosa sp 2**	0.67	-	8.63	-	66.10	-
Moderate grazing						
*Afropisaura rothiformis***	-	5.13	-	4.40	-	37.49
Ammoxenus amphalodes†	2.80	-	2.35	-	13.67	-
Araniella sp 1†	-	0.38	-	0.30	-	2.54
Cheiracanthium africanum†	-	0.75	-	0.42	-	3.55
Cydrela sp 1**	0.30	-	2.04	-	11.84	-
Leucage sp 1†	-	0.38	-	0.45	-	3.81
Monaeses pustulosus †	-	0.63	-	0.93	-	7.92
Monaeses quadrituberculatus	-	1.50	-	2.15	-	18.30
Pardosa sp 2**	1.1	-	8.90	-	51.72	-
Runcinia affinis †	-	0.50	-	0.46	-	3.92
Stenaelurillus sp 1‡	0.50	-	3.20	-	18.59	-
Thantus dorsolineatus ‡	-	0.75	-	0.32	-	2.77
Thyene sp 1‡	-	1.00	-	0.62	-	5.26
Tibellus sp 1‡	-	0.75	-	0.57	-	4.87
No grazing						
Aelurillus sp 1*	0.22	-	0.69	-	8.20	-
*Afropisaura rothiformis***	-	4.00	-	8.90	-	44.18
*Aphantaulax inornata**	-	0.60	-	2.07	-	10.29

Cydrela sp 1**	0.22	-	1.39	-	16.39	-
Evarcha sp 1†	-	1.10	-	2.23	-	11.04
Pardosa sp 2 **	0.78	-	5.44	-	64.24	-
Stenaelurillus sp 1‡	0.33	-	0.69	-	8.20	-
Suemus punctatus ‡	-	0.40	-	0.61	-	3.04
Thantus dorsolineatus‡	-	1.50	-	0.85	-	4.20
Thyene sp 1‡	-	1.40	-	1.48	-	7.34
Tibellus sp 1‡	-	1.10	-	2.37	-	11.75

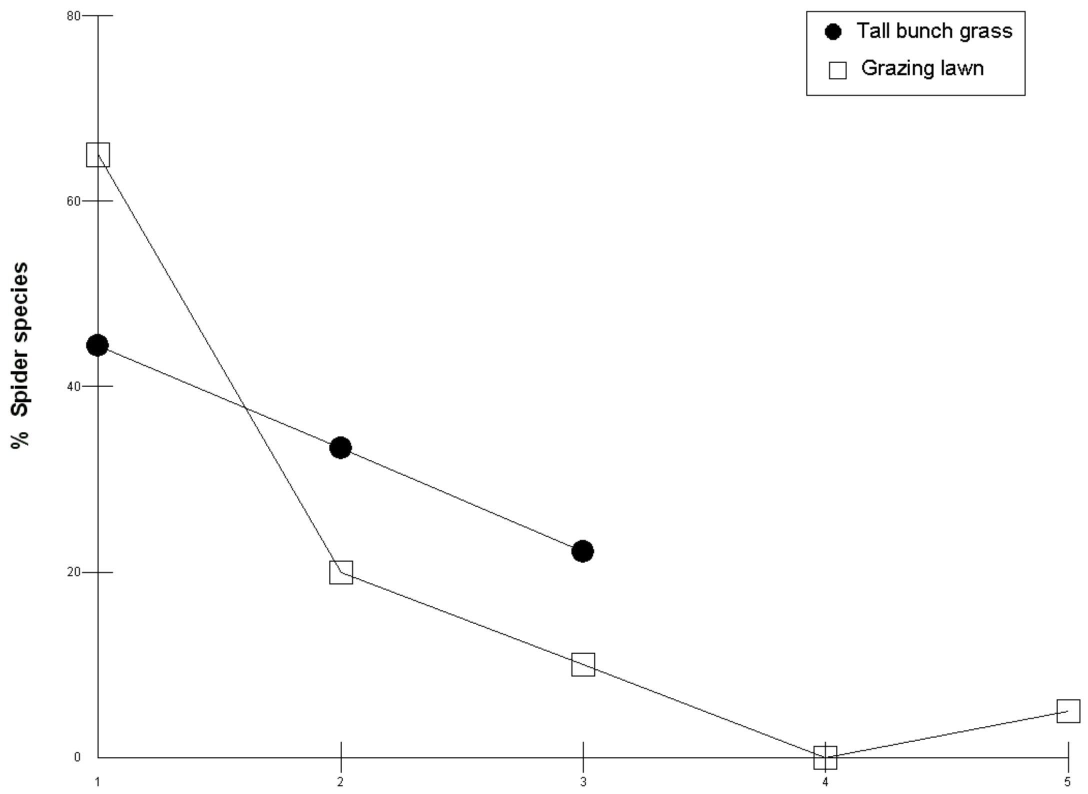

Fig. 4. Geometric class plot illustrating differences in the species compositional structure of the grazing lawn *versus* bunch grass type for the pitfall trap data sampled in HiP during September 2005.

Table 3. Unique spider species to the respective grazing intensity level, grassland type and sections in Hluhluwe-iMfolozi Park.

		Grazing intensity			**Grass type**		**Section**	
Family name	**Scientific name**	**Intense**	**Moderate**	**None**	**Grazing lawn**	**Tall bunch grass**	**Hluhluwe**	**iMfolozi**
Ammoxenidae	*Ammoxenus amphalodes*				x			x
Araneidae	*Araniella* sp 1						x	
	Araneus coccinella			x	x		x	x
	Araneus strupifer				x			
	Cyclosa insulana		x					
	Hypsosinga lithyphantoides			x			x	
	Hypsosinga sp 1			x			x	
	Hypsosinga sp 2			x	x		x	
	Hypsacantha sp 1			x	x		x	
	Pararaneus cyrtoscapus	x						x
	Pycnacatha tribulus	x			x		x	
Clubionidae	*Clubiona* sp 1							x
Corinnidae	*Corinnidae* sp 1			x			x	
Dictynidae	*Dictyna* sp 1							x
Gnaphosidae	*Setaphis* sp 1						x	
	Stenaelurillus sp 1		x				x	
	Camillina sp 1					x		
	Stenaelurillus sp 1					x		
	Zelotes oneili				x			
Idiopiidae	*Segregara pectinipalpis*		x				x	
Linyphiidae	*Linyphiidae* sp 1	x			x		x	
Lycosidae	*Evippomma squamulatum*				x			
	Hogna sp 1					x		x
	Hippasa australis	x				x		x
Miturgidae	*Cheiracanthium africanum*				x			
Nemesiidae	*Hermacha* sp 1			x	x			x
Oecobiidae	*Oecobius* sp 1			x	x		x	
Oxyopiidae	*Oxyopes* sp 1				x			x
	Oxyopes jacksoni			x				
	Oxyopes longispinosa		x		x			

Table 3 continued…...

		Grazing intensity			**Grass type**		**Section**	
Family name	**Scientific name**	**Intense**	**Moderate**	**None**	**Grazing lawn**	**Tall bunch grass**	**Hluhluwe**	**iMfolozi**
Oxyopiidae	*Oxyopes pallidecoloratus*		x					x
Philodromidae	*Philodromus* sp 1					x		
	Thanatus sp 1			x	x		x	
	Tibellus armatus					x		x
Pholcidae	*Spermophora* sp 1	x					x	
Pisauridae	*Afropisaura* sp 1							x
Prodidomidae	*Theuma foveolata*	x					x	
	Theuma fusca				x			
Salticidae	*Evarcha* sp 2							x
	Hyllus sp 1			x				x
	Pellenes sp 1		x				x	
	Pellenes sp 2		x				x	
	Phlegra sp 1	x					x	
	Stenaelurillus sp 1							x
Sparassidae	*Olios* sp 1			x		x	x	
Tetragnathidae	*Clitaetra irenae*		x		x		x	
Theridiidae	*Phoroncidia*			x				x
Thomisidae	*Heriaeus buffonii*	x			x			x
	Monaeses gibbus		x				x	
Thomisidae	*Monaeses pustulosus*				x			
	Monaeses quadrituberculatus				x			
	Oxytate argenteooculata		x					x
	Runcinia flavida				x			
	Stiphropella gracilis	x			x			x
	Synema nigrotibiale					x		x
	Tmarus sp 1	x						x
	Thomisops granulatus						x	
	Xysticus sp 1		x		x		x	
Zodariidae	*Caesetius* sp 1			x	x			x
	Cydrela sp 1				x			
	Diores sequax				x		x	

Table 3 continued…...

		Grazing intensity			Grass type		Section	
Family name	**Scientific name**	**Intense**	**Moderate**	**None**	**Grazing lawn**	**Tall bunch grass**	**Hluhluwe**	**iMfolozi**
Zodariidae	*Ranops caprivi*	x			x		x	
Total uniques		**10**	**13**	**15**	**30**	**9**	**27**	**25**

Table 4. SIMPER routine from pitfall trap (PT) and sweep net (SN) data from two grassland types in HiP, illustrating spider species that are characteristic and contribute to the overall similarities for each grassland type, average abundance of each species in each grassland type, similarity observed within each grassland type and the percentage contributed by each species to the similarity of a given grassland type. Symbols: * denotes species that are characteristic to both tall bunch grass and grazing lawns and † denotes species that are uniquely characteristic to each grass type.

Spider species per grassland type	**Average abundance of total**		**Average similarity of total**		**% contribution to similarity among grass type**	
	PT	SN	PT	SN	PT	SN
Tall bunch grass						
Aelurillus sp 1 *	0.60	-	8.21	-	20.57	-
*Afropisaura rothiformis**	-	4.80	-	7.43	-	32.70
Pardosa sp 2*	1.00	-	20.38	-	51.04	-
Thantus dorsolineatus †	-	2.40	-	3.97	-	17.44
Thyene sp 1†	-	1.80	-	10.16	-	44.69
Grazing lawns						
Aelurillus sp 1 *	-	0.33	-	1.90	-	13.87
*Afropisaura rothiformis**	-	1.67	-	4.25	-	30.96
Ammoxenus amphalodes	2.67	-	1.03	-	6.70	-
Diores sequax†	0.50	-	1.67	-	10.89	-
Evarcha sp 1†	-	0.67	-	1.01	-	7.38
Evippomma squamulatum†	0.67	-	1.03	-	6.70	-
Monaeses fuscus†	-	2.67	-	2.06	-	14.96
Monaeses pustulosus†	-	0.67	-	1.01	-	7.38
Monaeses quadrituberculatus†	-	0.50	-	2.87	-	20.93
Pardosa sp 2*	0.83	-	9.23	-	60.31	-
Stenaelurillus sp 1†	0.50	-	1.33	-	8.71	-

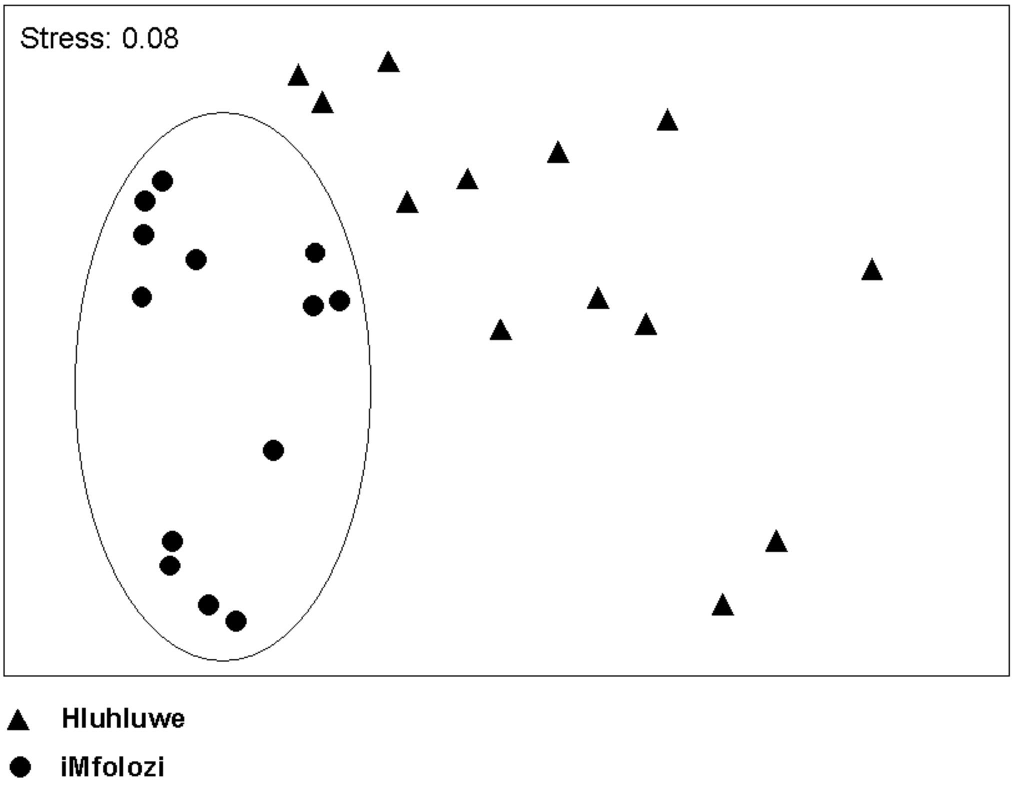

Fig. 5. Non-metric Multidimensional Scaling on Bray-Curtis similarities, to assess overall changes and similarity in spider assemblage composition in an area of high rainfall and altitude (Hluhluwe) and low rainfall and altitude (iMfolozi) based on pitfall trap data. The stress value of 0.08 and the ANOSIM indeed proved the plot to be significant (*R* = 0.493, *P* = 0.001).

Table 5. SIMPER routine from pitfall trap (PT) and sweep net (SN) data for areas of high (Hluhluwe) and low (iMfolozi) rainfall and altitude, illustrating spider species that are characteristic and contribute to the overall similarities for each area, mean abundance of each species in each area, similarity observed within an area and the percentage contributed by each species to the similarity of the section. Symbol: † denotes unique characteristic species to each area.

Spider species per Section	**Mean abundance of total**		**Mean similarity of total**		**% contribution similarity among areas**	
	PT	SN	PT	SN	PT	SN
Hluhluwe						
Aelurillus sp 1†	0.31	-	1.47	-	9.02	-
Afropisaura rothiformis	-	1.25	-	4.04	-	38.21
Aphantaulax inornata†	-	0.33	-	1.14	-	13.31
Araniella sp 1†	-	0.50	-	0.86	-	8.12
Camillina sp 1†	0.31	-	1.70	-	10.45	-
Evarcha sp 1	-	0.33	-	0.63	-	5.95
Hogna sp 1†	0.31	-	1.03	-	6.31	-
Monaeses pustulosus†	-	0.50	-	0.57	-	5.38
Monaeses quadrituberculatus	-	0.50	-	0.37	-	3.48
Pardosa sp 2	1.00	-	11.20	-	68.82	-
Runcinia affinis†	-	0.42	-	0.71	-	6.70
Thyene sp 1	-	0.25	-	0.44	-	4.12
Tibellus sp 1	-	0.50	-	0.53	-	5.02
iMfolozi						
Afropisaura rothiformis	-	6.79	-	9.65	-	49.13
Ammoxenus amphalodes†	3.73	-	5.82	-	29.13	-
Asemesthes ceresicola†	0.60	-	1.76	-	8.80	-
Cydrela sp 1†	0.33	-	4.67	-	23.35	-
Evarcha sp 1	-	1.43	-	0.93	-	4.74
Monaeses fuscus†	-	0.36	-	0.49	-	2.51
Monaeses quadrituberculatus	-	0.71	-	0.54	-	2.76
Oxyopes sp 1†	-	1.93	-	1.93	-	9.84
Pardosa sp 2	0.73	-	4.75	-	23.77	-
Stenaelurillus sp 1†	0.47	-	2.53	-	12.64	-
Thantus dorsolineatus†	-	1.50	-	1.32	-	6.72
Thyene sp 1	-	1.57	-	1.44	-	7.31
Tibellus sp 1	-	0.86	-	1.54	-	7.82

Discussion

WHAT IS THE IMPACT OF GRAZING INTENSITY GRADIENTS?

Results showed different spider response to grazing intensity gradients. High abundance, diversity and richness were noted under moderate and intense grazing pressure. On the contrary, low abundance, diversity and richness were consistently observed in ungrazed sites. No significant differences were observed between moderately grazed and intensely grazed sites. However, significant differences were observed with moderately grazed sites and ungrazed sites, with ungrazed sites consistently illustrating the lowest diversity and species richness.

This finding can perhaps be explained by the reason that grazed sites have higher structural complexity with high litter layers (Gibson *et al.* 1992b), more vegetation cover (Seymour & Dean 1996) and higher plant diversity (Rambo & Faeth 1999), which ultimately result in increased invertebrate diversity (Gibson et *al.* 1992b; Rambo & Faeth 1999; Mclyntyre 2005). Furthermore, studies show that the effect of grazing on arthropod assemblages varies between studies and geographical area.

Abensperg-Traun *et al*. (1996) showed a significant increase in arthropod abundance and species richness with moderate grazing when comparing intense, moderate and low grazing intensity pressure. Seymour & Dean (1996) showed higher species richness in various invertebrate groups with moderate grazing intensity *versus* intense grazing intensity. Gisbon, Brown & McGavin (1992b) also showed a decline in spider species richness as the grazing intensity increased, while Morris (1968) showed a decline in spider abundance. Moreover, González-Megías, Gómez & Sànchez-Piñero (2004) showed a decline in spider species richness and diversity with no grazing.

The ungrazed sites (Table 3) were the only sites inhabited by Theridiidae specialists of moist habitats (Harris, York and Beathie 2003) and Nemesiidae, which inhabit woody litter

(Abensperg-Traun *et al*. 1996). This suggests that due to more aerial cover (Seymour & Dean 1996) and accumulation of litter (Gibson *et al.* 1992b), the microhabitats created in these sites allow these specialists to colonise. Furthermore, as low disturbance frequency allows specialists to colonize (Connell 1978) the highest number of unique species was found in ungrazed sites. Spiders from the family Linyphiidae (Table 3), which are characteristic of disturbed environments (Abensperg-Traun *et al*. 1996), were only found in intensely grazed sites.

Interestingly, there were no significant differences in guild structures with grazing intensity levels. This finding has also been reported by Harris, York and Beathie (2003) who found no differences in spider guild structures between grazed and ungrazed sites. Gibson, Hambler & Brown (1992b) suggested that spider assemblages may be unaffected by grazing pressure to a certain extent.

DO GRAZING LAWNS SUPPORT A DISTINCT SPIDER ASSEMBLAGE PATTERN?

Grazing lawns do support high species richness of birds, insects, plants (Bond, Smythe & Balfour 2001; Currie 2003; Krook 2005) and spiders, which opposes the assumption that they are a result of overgrazing and thus highly undesirable. In this study grazing lawns displayed the highest spider diversity and species richness. Similarly, Krook (2005) found significantly higher bird species richness and diversity in grazing lawns in comparison to tall bunch grasses, and Currie (2003) postulated that grazing lawn is crucial to some stages in the lifecycle of certain species of grasshoppers and thus essential for reproductive success. The grazing lawns of this study had the highest number of singletons and thirteen species were found unique to this grass type. This is further evidence in support of Currie (2003) and Krook's (2005) conclusion that grazing lawn grass types have a distinct grass and fauna assemblage pattern and are unique communities and not a sub-set of any other grassland type or an undesirable outcome of overgrazing. Consequently, there is now growing evidence that these grazing lawns do feature in our natural history.

Numerous herbivores have been shown to prefer these short grass grazing lawn habitats; for example warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), black rhinoceros (*Diceros bicornis*) (Bond, Smythe & Balfour 2001), white rhinoceros (*Ceratotherium simum*), blue wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus burchelli*) (Archibald *et al.* 2005). Currie (2003), on studying the impact of megaherbivore grazers on grasshopper communities in the same exclosure sites that were used in this study, postulated that the lawn patches in the Park may play an important role in maintaining biodiversity.

WHAT ARE THE EFFECTS OF VARYING ALTITUDE AND RAINFALL?

Two distinct assemblage patterns were observed for the sites varying in altitude and rainfall but different species regional pools are difficult to prove. Interestingly, 14% of the spider species captured in iMfolozi were from the family Ammoxenidae, *Ammoxenus amphalodes* and none were captured from Hluhluwe. This family inhabits sandy soils, semi-arid desert and in association with termites (Dippenaar-Schoeman & Jocquè 1997). Therefore the results do show that altitude and rainfall are important factors that inter-play in spider species compositional structures. More than double the numbers of specimens were captured in iMfolozi in comparison to Hluhluwe. There could a number of underlying factors owing to this trend, however higher grazing intensity in iMfolozi than in Hluhluwe could equally be a contributing factor (van Rensburg, pers.comm). However, non-exhaustive sampling due to the sampling duration may have also attributed to the higher number of species exclusive to both sites.

Conclusions and management applications

Moderate and intense grazing pressure resulted in the highest abundance, diversity and species richness of spiders in this study. The ungrazed sites had lower abundance, species richness and diversity, implying that no grazing has negative consequences for biodiversity. Currie (2003) and Waldram (2005) showed significant differences in grass height and aerial cover among the different grazing intensity levels in these sites, where the ungrazed sites were shown to be characteristic of tall bunch grassland type and the grazed sites were characteristic of grazing lawns. Grazing lawns support unique spider species; they are stable state communities on their own and not an undesirable subset of any other grassland type. In light of this, veld management decisions that eradicate grazing lawns are negative for the park and its biodiversity, as the loss of the grazing lawns with time may lead to cascading effects on biota that are associated with this grass type, i.e. some grazers, birds, insects and plants (Archibald *et al.* 2005). Grazing lawn formation is assisted by low frequency fire regimes and/or high herbivore numbers (Krook 2005).

Though spiders are good bioindicators, as they show simple responses to disturbance and are less likely to fluctuate than other invertebrate taxa, there is a limit to the amount and type of information that a single invertebrate group can give about the whole fauna (Gibson, Brown & McGavin 1992b). Savanna biomes are very important for the preservation of invertebrate biodiversity as they support a higher diversity than other biomes that have been surveyed in South Africa (Whitmore *et al.* 2002). Thus, further research should be encouraged in the savanna biome and factors affecting spider assemblages other than habitat type need to be identified as to their important influence on spider diversity (Whitmore *et al*. 2002). By the identification of spatial and temporal communal patterns of spiders in different habitat types and correlating these with other certain variables one can produce a workable outlay for recognising relevant questions and hypotheses that concern community structure and ecosystem functioning (Van der Merwe 1994). This study promotes a mosaic of all grass types and structural heights as various species are associated with different grass types and grazing intensity levels.

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CHAPTER 3

Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management

Abstract

1. Invasions by alien plants into unspoiled ecosystems are a cause for concern because the pristine systems are important stores of biodiversity. Indeed, the introduction of non-indigenous species into protected areas is a direct threat to conservation. Consequently, it is fundamental to document the impact that alien invasive plants have on native communities and to determine if, and at what rate, native communities re-establish following the removal of invasives

2. *Chromolaena odorata* is one of the most important invader species in the savannah biome in South Africa. It reduces vegetation heterogeneity in grasslands, savannahs and forests.

3. Spiders as ecological indicators for change were used to investigate the impact of (i) *C. odorata* invasions (ii) *C. odorata* invasion durations and (iii) the impact of clearing *C. odorata* on abundance, assemblage patterns, diversity and estimated species richness.

4. The progressive invasion of *C. odorata* with increasing invasion duration brings with it changes in native spider abundance, assemblage patterns, diversity and estimated species richness. Native spider assemblages do re-establish after clearing *C. odorata* without further management intervention. Small lingering differences are observed between the native and the cleared sites suggesting that other features of the habitat may have been affected by the invasion and clearing.

5. *Synthesis and applications*. Alien clearing is clearly an essential and invaluable management tool. There are a substantial number of programmes that aim to eradicate alien invasive plants, but, very little is known about how biodiversity recovers after alien plant removal. Thus, our data show that the removal of alien invasive plants benefits biodiversity with immediate effects, highlighting that management to should eradicate this invasive should be done, even if the area has been invaded for a long period of time These data are important for policy forming and informing policy makers that aliens and their clearing are critical for biodiversity conservation management.

Key-words: Alien invasive plant, biodiversity, habitat structure, Hluhluwe-iMfolozi, pitfall traps, South Africa, species richness.

Introduction

South Africa is one of the countries most seriously affected by alien plant invasions (Richardson & van Wilgen 2004). Invasive weeds alter vegetation structure in the areas they invade leading to lower native plant species richness (Knops *et al*. 1999). Some invasive species may also be considered ecological engineers as they modify the ground surface micro-environment in encroached areas (Pétillon *et al.* 2005). Invasions by alien plants into unspoiled ecosystems are a cause for high concern because the pristine systems are important stores of biodiversity (Higgins *et al*. 1999). Indeed, the introduction of non-indigenous species into protected areas is a direct threat to conservation (Blossey 1996). Consequently, it is fundamental to document the impact that alien invasive plants have on native communities and to determine if, and at what rate, native communities re-establish following the removal of invasives (Gratton & Denno 2005). A thorough understanding of an invasion is necessary for the development of basic ecological principles used for its management (D'Antonio & Vitousek 1992). Since the effect of invasive species can be slow and cumulative, extending over time, most studies on the effects of invasive species lack a temporal context (Strayer *et al*. 2006).

Triffid weed, *Chromolaena odorata* (L) R.M. King and H. Robinson (Asteraceae) is native to South and Central America. It grows rapidly and forms impenetrable tangles that may ultimately shade out all the indigenous vegetation (Macdonald 1983). Through physical smothering and allelopathy *C. odorata* reduces vegetation heterogeneity in grasslands, savannahs and forests (Goodall & Zachariades 2002). *Chromolaena odorata* has naturalized in many parts of the world (Ambika & Jayachandra 1990) and has been noted as one of the most important invader species in the savannah biome in South Africa (Richardson & van Wilgen 2004). Robertson *et al.* (2003) ranked *C. odorata* as the second worst alien weed species to cause problems in South Africa after Lantana *Lantana camara* L. Accordingly, *C. odorata* has become a major problem in conservation areas and is the most wide-spread invader posing the greatest threat to the natural vegetation in Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal in South Africa (Macdonald 1983; Howison & Balfour 2002). *Chromolaena odorata* was first recorded in HiP in 1961. In 1983 the distribution of *C. odorata* was mapped for the first time revealing 50 ha of infestation (Macdonald 1983). Re-mapping in 1998 showed 2 100 ha of infestation (Howison & Balfour 2002).

There is an intimate association between most arthropods and native vegetation or the microhabitats it creates (Greenwood, O'Dowd & Lake 2004; Gratton & Denno 2005). Any decrease in the dominant plant species and/or alteration of physical characteristics of the habitat is anticipated to have negative consequences for the indigenous fauna (Greenwood, O'Dowd & Lake 2004; Gratton & Denno 2005). Since native insects share little or no evolutionary history with alien plants they may not be adapted to use these plants for food (Tallamy 2004). Subsequently, theory predicts that the solar energy stored by alien plants is largely unavailable to indigenous specialists in ecological time and thus unavailable to higher trophic levels that include these insects in their diets (Tallamy 2004). Spiders are at the top of their terrestrial arthropod communities and are expected to integrate the biotic and abiotic influences affecting lower trophic levels (Scott, Oxford & Selden 2006). They are good ecological indicators for change (Gibson *et al*. 1992a; Gibson, Hambler & Brown 1992b; Longcore 2003; Scott, Oxford & Selden 2006), and therefore good for assessing the effects of management startegies (Gibson *et al*. 1992a). Furthermore, due to their short generation times, spiders are ideal for observing year-to-year changes in sites (Longcore 2003). Spiders are also efficient monitors of slight but important variations that have the potential to influence habitat quality as they occupy the widest diversity of microhabitats and niches (Foelix 1982; Longcore 2003). Any change in the spider community reflects even larger changes in the habitat and the arthropod herbivore community that supports spiders. Spiders, therefore only interact with alien plants indirectly.

In the light of the above, this study aims to investigate the following three questions: 1) Do *C. odorata* invasions alter native spider assemblage patterns? 2) Do different invasion durations of *C. odorata* have a varying effect on native spider assemblage patterns? And lastly, 3) do native spider assemblages re-establish after *C. odorata* clearing without further management intervention? This study aims to give a better understanding of how *C. odorata* invasion durations and its clearing affect biodiversity using spider responses. The questions posed in this study are of utmost importance, because more invasive species are colonizing non-native countries and more clearing projects being put in place (Samways, Taylor & Tarboton 2005). These data are important for policy forming and convincing policy makers that aliens and their clearing are critical for biodiversity conservation management.

Materials and methods

STUDY AREA

Data were collected from Hluhluwe-iMfolozi Park, which lies between the latitudes 28°00’ and 28°26’S and longitudes 31°43’ and 32°09’ E. HiP is located in the foothills of the escarpment to the west of the coastal plain in central KwaZulu-Natal, South Africa. It encompasses 900 km^2 and is comprised of a northern section, Hluhluwe (300 km^2) and a southern section, iMfolozi and corridor (600 km^2). This Park has unimodal rainfall (Macdonald 1983); the mean annual rainfall is 990 mm in Hluhluwe and 720 mm in iMfolozi (Whateley & Porter 1983). The environment and the vegetation of this park are described by Whateley & Porter (1983).

EXPERIMENTAL DESIGN AND SAMPLING METHODS

Using historical maps of the distribution of *C. odorata* in the northerly, wetter region of HiP (provided by Ezemvelo KZN Wildlife), six treatments with differing *C. odorata* invasion durations and differing clearing times were selected. These treatments included one that had recently been invaded (*ca* 2 years); two that had been invaded for a longer period (*ca* 10 years and *ca* 20 years); a treatment that had recently been cleared (cl 2 years); a treatment that had been cleared for a longer period (cl 3-5 years); and finally, as a control, a treatment that had no history of *C. odorata* invasion. The treatments were located in white Stinkwood *Celtis africana* dominated areas, giving a similar vegetation type for all treatments. In the cleared areas *C. odorata* had been removed by Department of Water Affairs and Forestry & Ezemvelo KZN Wildlife staff. These areas were cleared by hand pulling, applying foliar spray to seedlings (Triclopyr) and by cutting mature stumps and then applying herbicide (Imazapyr). Areas with similar aspect and position in the catena were selected. Six replicate sites per area were selected, giving of 36 sample sites. The replicate sites within the treatment areas were a minimum of 200 m apart. All sampling effort for this study was repeated seasonally for a year, making a total of four seasonal spider sampling sessions (January, April, June and October). All seasonal samples were summed for an overall mean at each site. All specimens were identified to species and morphospecies. Voucher specimens are deposited in the National Collection of Arachnida at the Agricultural Research Council - Plant Protection Research Institute, Pretoria.

Pitfall traps

Spiders were sampled using pitfall traps. Within each of the 36 treatment sites (including control), 10 pitfall traps were set up in a rectangular grid (2 m x 8 m) with 2 m spacing between traps (n = 360 traps per sampling session). Small plastic cylindrical vials (3.5 cm across and 13.0 cm deep) were sunk into the ground so that the lip of the vial was flush with the ground surface (Gibb & Hochuli 2002; Sørensen *et al.* 2002). The vials were left open in the ground and filled with approximately 2 cm, 50/50 mixture of water/ propylene glycol and a few drops of liquid soap, then allowed to stand out for 72 hours. The spiders were then collected from the traps and separated from other invertebrates and stored in 70 % ethanol.

Vegetation beating

To determine if there were any species not covered by the pitfall traps but which had temporal changes, *C. odorata* was sampled by vegetation beating. This was used as the second sampling method because it targets fauna from low vegetation (Sørensen *et al*. 2002) while the pitfall traps samples mostly ground dwelling spiders. As no vegetation beating was done in the control area, data from the two sampling methods were analysed separately so as to allow correct interpretation. In each of the 30 sites where *C. odorata* was present 10 *C. odorata* plants were randomly selected within a range of 20 x 20 m. The spiders were collected at all sites by the same person (MPG) by tapping the vegetation six times with a heavy stick while holding a 570 mm x 410 mm collecting tray underneath. The spiders were separated from other invertebrates and stored in 70 % ethanol.

DATA ANALYSES

The data from the two sampling methods were analysed separately as they are designed to target different assemblages and because no vegetation *(C. odorata)* beating was done in the control sites. Species accumulation curves for the two sampling methods were used to determine sampling adequacy. Because the data could not be transformed to be normally distributed, non-parametric tests Mann-Whitney U (*U*) and Kruskral-Wallis Analysis of Variance (*H*) (ANOVA) were applied to the data with the software programme STATISTICA v6 (http://www.statsoft.com). Non-parametric species richness estimators were computed using the EstimateS v7 software programme (http://viceroy.eeb.uconn.edu/estimates). To examine differences in spider assemblages between the different sites, the following diversity indices were calculated using the PRIMER v5 software (Plymouth Routines In Multivariate Ecological Research) (Clarke

& Warwick 2001): total number of specimens (N), alpha diversity (S), Shannon-Wiener (H'), Simpson's (1-λ) and Margalef's (d) (Clarke & Warwick 2001).

Similarities among habitats were calculated using a Bray-Curtis similarity index on fourth root-transformed data to down-weigh the most abundant species and to take into account rare species (Clarke & Warwick 2001). Non-metric Multidimensional Scaling (nMDS) ordination analyses in PRIMER 5 were used to establish if there were assemblage patterns owing to invasion and clearing duration. To improve the stress value and interpretation of the nMDS outliers were excluded (Clarke & Warwick 2001). Analyses of similarity (ANOSIM) were further used to establish if there were significant differences in spider assemblages observed due to invasion duration and clearing duration. Similarity percentages (SIMPER) routines were used to determine which species contributed to the observed patterns of species distributions in the different sites.

Geometric class plots were used to determine differences in species classes between the cleared sites, where species abundance distributions were assessed. Geometric class plots are frequency polygons for a pooled set of samples and number of species fall into a set of geometric abundance classes. These were plotted by the number of classes represented in the sample i.e. 1 individual — class 1; 2-3 individuals — class 2; 4-7 individuals — class 3; etc. Since spiders live in defined environments and have limitations set by physical conditions and biological factors (Foelix 1982), their species can be grouped into guilds based on the available information on their preferred habitats and predatory strategies (Dippenaar-Schoeman *et al.* 2005). Therefore the spiders were allocated to their guilds primarily using Dippenaar-Schoeman *et al.* (2005) and secondarily Dippenaar-Schoeman & Jocquè (1997). The guilds they were allocated can be divided into two main groups namely web builders (WB) and wanderers (W). The web builders construct the following types of webs: funnel-web (FWB); orb-webs (OWB), sheet-webs (SWB), gumfoot-webs (GFWB). The free-living wanderers were defined as: free-living ground-dweller (GD) and burrowing ground dweller (BGD) and plant-dwellers (PD) (see Appendix D).

Results

A total of 825 spiders, making up 106 species in 30 families were captured. From the pitfall traps 449 individuals from 68 species in 24 families were caught while 380 individuals from 66 species in 20 families were retrieved by vegetation beating. The species accumulation curves showed that, as was to be expected, further sampling would have resulted in a greater number of captured species/individuals. However, the curve increase diminished with increasing number of samples, particularly for the pitfall trap data, illustrating that most of the common species were captured. For both sampling methods, 35 % of the spider species were singletons (species represented by a single individual) and 10 families (33 %) were represented by fewer than five individuals. The most species-rich families were the Araneidae (17 species), Salticidae (15 species), Thomisidae (14 species), Lycosidae (11 species) and the Gnaphosidae (10 species). The most abundant families were the Lycosidae (241 individuals), Salticidae (132 individuals), Thomisidae (92 individuals), Gnaphosidae (60 individuals) and the Araneidae (47 individuals). A total of 22 species (9.94%) were web builders and 138 species were wanderers (90.06%).

Do *C. odorata* invasions alter spider assemblage patterns?

The control sites had the highest abundance, alpha diversity, Margalef's diversity and Shannon-wiener diversity for pitfall trap data in comparison to sites invaded with *C.*

odorata for different invasion durations and to cleared sites (Table 1). These results proved not to be significant; however Fig. 1a demonstrated the trend that the control sites had higher species richness than invaded sites. Of interest was that both sites that have been invaded for the longest duration had similarly lower species richness (Fig.1a).

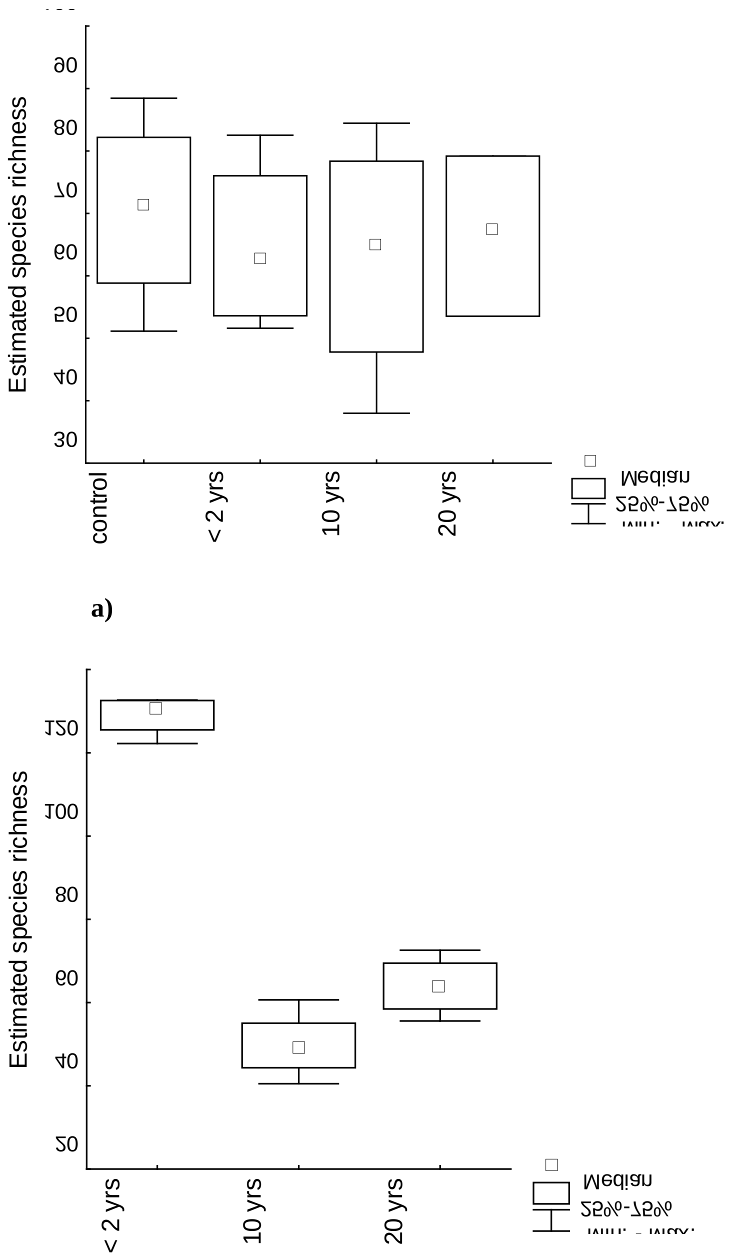
Do different invasion durations of *C. odorata* have a varying effect on native spider assemblage patterns?

As anticipated, with increasing invasion duration the pitfall trap data showed (from new invasion to 20 yr invasion) an overall declining trend in abundance and alpha diversity of spiders caught (Table 1). As vegetation beating was designed to observe if there were any spider species that inhabited this invasive weed, the 10 yr invasion sites had the highest abundance with the newly invaded sites (< 2 yrs) having the lowest abundance (Table 1). Interestingly, similarly to pitfall trap data, the vegetation beating data showed the higher diversity to be in the newly invaded sites and the lowest in the sites that have been invaded for longer durations (Table 1).

The observed differences from the diversity indices in Table 1 were not significant However, non-parametric species richness estimators (Jacknife second order) further showed a similar trend of richness declining with invasion duration for pitfall trap data (Fig. 1a) and vegetation beating data further proved these trends to be significant ($H_{2,12} = 9.269$, $P < 0.01$) (Fig. 1b). The site that had been invaded for 20 years had the highest overall contribution of Zodariidae which is a specialist in disturbed habitats and the 10 years invaded site had the highest overall contribution of Salticidae which is a generalist tolerant of dry habitat (see Appendix D). The MDS ordination revealed significant differences in spider assemblage patterns due to different invasion durations (Fig. 2) ($R = 0.442$, $P < 0.01$). Moreover, there were no significant differences between the sites

Table 1. Diversity index values in the control sites in comparison to the invaded for less than 2 years, 10 years and 20 years, and cleared sites for 2 years and 5 years. Values are means of diversity indices per site (pitfall traps = PT; vegetation beating = VB): S = alpha diversity; N = abundance (number of individuals); d = Margalef's; H' (loge) = Shannon & 1 -λ = Simpson's. Note: As there was no *Chromolaena odorata* within the control sites there are no data available for vegetation beating for this treatment.

	Control	< 2 yrs		10 yrs		20 yrs		cl 2 yrs		cl 5 yrs	
Diversity index	PT	PT	VB	PT	VB	PT	VB	PT	VB	PT	VB
N	24.0	23.0	19.0	20.0	8.00	7.0	17.30	18.0	29.00	17.0	19.00
S	11.25	10.25	12.50	7.00	6.00	5.75	11.50	8.47	13.00	8.44	11.30
D	3.26	3.00	4.01	2.16	2.04	2.30	3.69	2.69	3.55	2.70	3.50
H'(loge)	1.92	1.79	2.40	1.49	1.36	1.59	2.27	1.71	2.25	1.72	2.16
1- λ	0.80	0.75	0.94	0.75	0.63	0.89	0.93	0.81	0.90	0.81	0.90



b)

Fig. 1. Estimated species richness with invasion duration for **a)** pitfall trap data ($H_{3,15}$ = 0.175, $P > 0.05$) and **b)** vegetation beating data ($H_{2,12}$ = 9.269, $P < 0.01$)

that were invaded for longer durations amongst themselves, however, significant differences were observed when comparing the sites that have been invaded for longer durations to sites that have been newly invaded (Fig. 2). SIMPER routine further revealed that the newly invaded sites (< 2 yrs) had the highest number of spider species uniquely characteristic to these sites (Table 2) and no significant differences in spider guild structures were observed when comparing sites of different invasion durations.

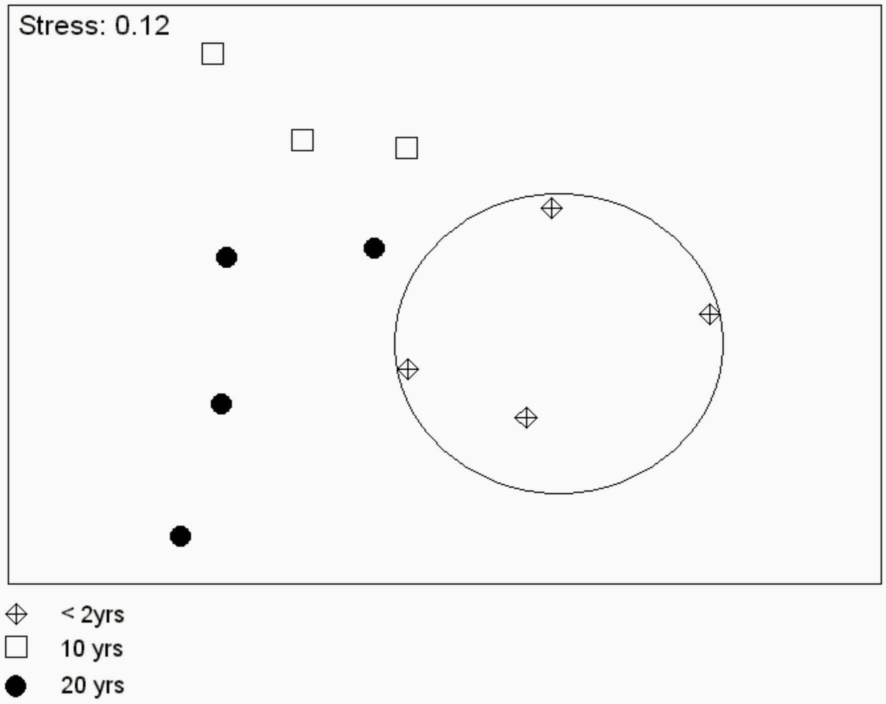


Fig. 2. Multidimensional scaling ordination based Bray-Curtis similarity matrix derived from fourth root transformed ground-dwelling spider data demonstrating different spider assemblages due to different invasion durations. The plot is significant (*R* = 0.442, *P* < 0.01), the pair wise tests revealed significant differences between the new invasion < 2 years and 10 years invasion (*R* = 0.667, *P* = 0.029) and no significant differences between 10 years invasion and 20 years invasion.

Table 2. Spider species contributions to similarities within the different sites (pitfall traps = PT; vegetation beating = SW). Av. Abund = average abundance (of total); Av. Sim = average similarity (of total); Contrib% = percentage contribution by the species to similarity among the different sites. Where: n/a denotes that no vegetation beating was done■, uniquely characteristic to control and either/both cleared sites, ▲ characteristic to all sites, ● uniquely characteristic to that site as indicated by PT, ☼ uniquely characteristic to that site as indicated by VB.

	Av. Abund		Av. Sim		Contrib%	
	PT	VB	PT	VB	PT	VB
Control						
Anahita sp 1■	1.25	n/a	2.11	n/a	7.35	n/a
Cydrela sp 1■	1.75	n/a	2.63	n/a	9.15	n/a
Hogna sp 1▲	5.75	n/a	9.40	n/a	32.67	n/a
Pardosa sp 1▲	6.25	n/a	11.76	n/a	40.88	n/a
< 2 yrs						
Araneilla sp 1	-	0.50	-	1.11	-	3.64
Asemesthes ceresicola●	0.75	-	2.23	-	8.68	-
Cheiracanthium vansoni	-	1.75	-	6.34	-	20.78
Clubiona sp 1	-	1.00	-	3.34	-	10.95
Cyphalonotus larvatuss☼	-	0.50	-	1.04	-	3.40
Heliophanus sp 1☼	-	0.50	-	1.19	-	3.90
Lycosa sp1●	0.75	-	2.42	-	9.45	-
Olios sp 2●	-	0.50	-	1.04	-	3.41
Pardosa sp 1▲	6.25	-	7.64	-	29.78	-
Stenaelurillus sp 1●	1.00	-	2.23	-	8.68	-
Thyene inflata	-	2.50	-	12.31	-	40.30
Tmarus cameliformis	-	0.50	-	1.19	-	3.90
10 yrs						
Olios correvoni	-	2.00	-	2.96	-	7.18
Pardosa sp 1 ▲	2.25	-	10.41	-	34.11	-
Setaphis sp 1	-	1.00	-	1.75	-	4.24
Thyene inflata	-	7.25	-	19.84	-	48.13
Thomisops pupa	-	2.25	-	3.50	-	8.49
Tmarus cameliformis	-	1.25	-	1.39	-	3.37
20 yrs						
Araneilla sp 1	-	0.50	-	1.15	-	6.32
Caesetius sp 1●	0.50	-	0.98	-	4.52	-
Evarcha sp 1	-	1.00	-	0.71	-	3.90
Heriaeus buffonii ●	0.50	-	0.98	-	4.52	-
Hogna sp 1▲	2.00	-	8.38	-	38.61	-
Olios correvoni	-	1.25	-	1.15	-	6.32
Pardosa sp 1▲	2.75	-	2.74	-	12.65	-

Synema nigrotibiale☼	-	0.50	-	0.72	-	3.98
Thomisops pupa	-	1.00	-	1.33	-	7.33
Tmarus cameliformis	-	2.25	-	3.83	-	21.07
Zelotes tuckeri	1.25	-	7.23	-	33.31	-

Table 2 continued….

cl 2 yrs						
Araneus sp 1 ☼	-	1.00	-	2.90	-	19.64
Cheiracanthium vansoni	-	1.00	-	2.90	-	19.64
Clubiona sp 1	-	1.00	-	6.06	-	41.07
Hogna sp 1 ▲	4.25	-	6.82	-	26.52	-
Pardosa sp 1▲	8.59	-	12.87	-	50.10	-
Thyene inflata	-	0.67	-	2.90	-	19.64
cl 5 yrs						
Anahita sp 1 ■	1.50	-	2.19	-	8.51	-
Araneilla sp 1	-	1.00	-	0.83	-	2.97
Cheiracanthium vansoni	-	1.00	-	2.94	-	10.50
Clubiona sp 1	-	1.00	-	1.55	-	5.53
Corinnidae sp 1•	-	0.50	-	1.15	-	4.10
Cydrela sp 1 ■	1.00	-	2.90	-	11.27	-
Diaea puncta •	-	1.00	-	0.83	-	2.97
Evarcha sp 1	-	1.00	-	2.68	-	9.57
Hogna sp 1▲	4.25	-	6.82	-	26.52	-
Olios correvoni	-	0.75	-	2.68	-	9.57
Pardosa sp 1 ▲	1.50	-	12.87	-	50.10	-
Thomisops pupa	-	1.25	-	3.44	-	12.27
Thyene inflata	-	3.00	-	8.80	-	31.42
Thyene natalii ☼	-	0.75	-	0.83	-	2.97
Anahita sp 1	0.75	-	3.88	-	12.70	-
Evarcha sp 1	-	2.50	-	5.04	-	12.23
Hogna sp 1 ▲	5.00	-	15.26	-	49.97	-
Anahita sp 1	0.75	-	3.88	-	12.70	-

Do native spider assemblages re-establish after *C. odorata* clearing without further management intervention?

Again, as anticipated, results showed that the clearing of this weed has an immediate positive effect on the abundance, diversity and estimated species richness of spiders. Illustrating the positive impact of clearing were the non-significant differences observed for diversity (Table 1) and estimated species richness (pitfall trap data) (Fig. 3).

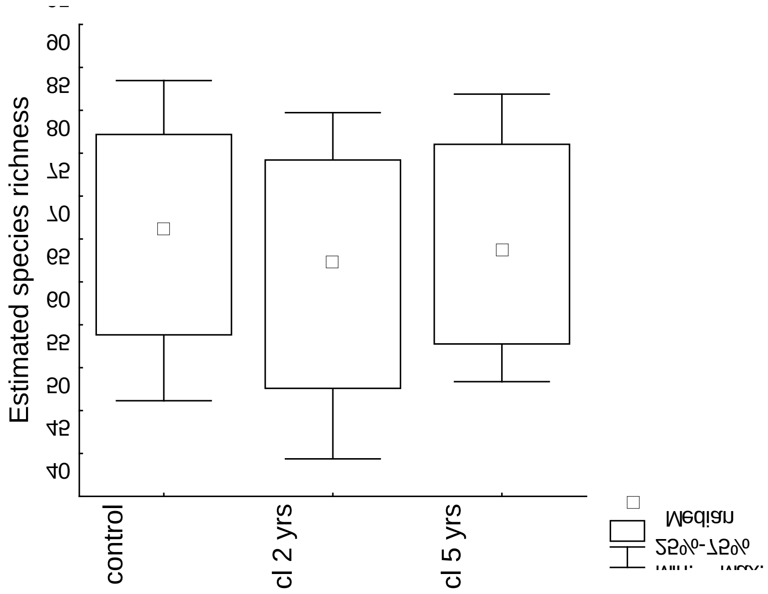


Fig. 3. Estimated species richness for the cleared sites for pitfall trap data ($H_{2,12} = 0.5000$, $P > 0.05$) illustrating non-significant differences to the estimated species richness of the control sites in comparison to the cleared sites.the cleared sites and the control.

Furthermore, ANOSIM demonstrated high similarity between the control sites and the cleared sites (Fig. 4) as there were no significant differences ($R = -0.174$, $P > 0.05$) with the negative *R* value denotes that these sites could be from the same sample. Also, no significant differences for guild structures were observed when comparing the cleared sites to the control sites. However, the results further show that, although the system is rehabilitating after *C. odorata* clearing, there are two families that occurred only in the control, namely Cyrtaucheniidae (trap door spider) and Liocranidae (moist habitat specialist) (see Appendix D).

Of interest was the high estimated species richness (Fig. 5) and abundance (Fig. 6a) in re-established *C. odorata* sites that have been cleared for a longer duration (cl 5 yrs) than

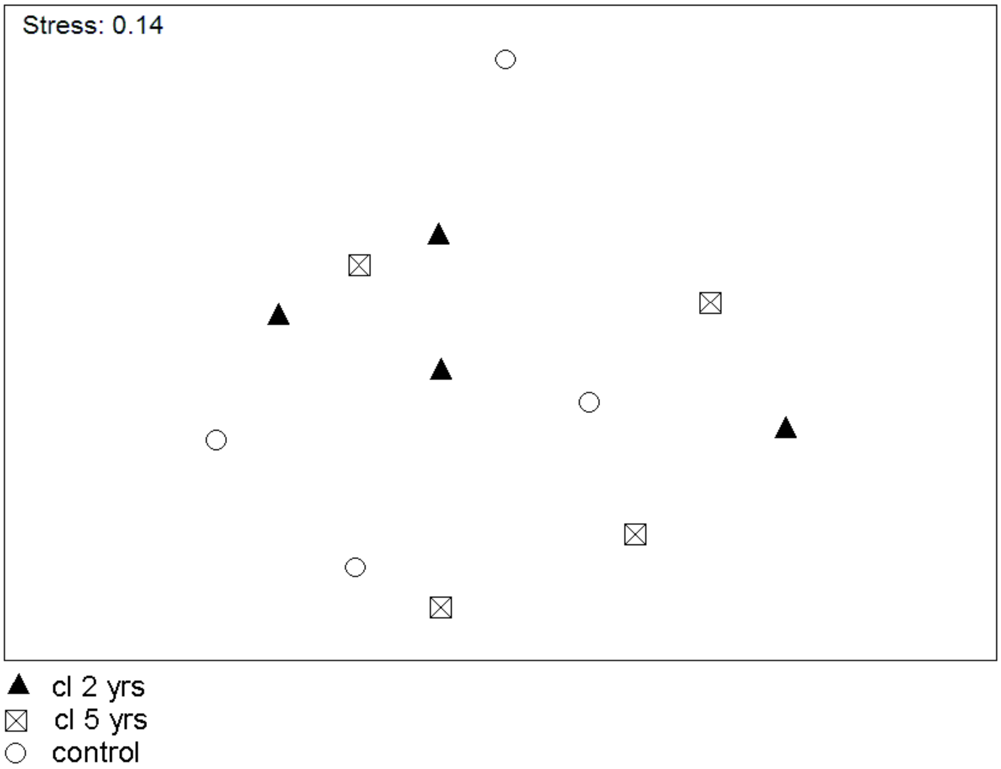


Fig. 4. Multidimensional scaling ordination based on fourth root transformed ground-dwelling spider data demonstrating similarity in spider assemblages in the control and the cleared sites (R = -0.174, $P < 0.01$) where the negative value denotes that these sites could be from the sample population.

recently cleared sites (cl 2 yrs). Of more interest was the significantly higher abundance of spiders in the control sites, than the recently cleared sites (cl 2 yrs) and the least in the sites cleared for a longer duration (cl 5 yrs) for pitfall trap data (Fig. 6b). Recently cleared sites (cl 2 yrs) have a higher percentage of rarer species when compared to the sites that have been cleared for a longer duration (cl 5 yrs) as shown by the geometric class plot for vegetation beating data. However, the sites cleared for a longer duration (cl 5 yrs) had more spider species in different class ranges (Fig. 7a). Essentially, the pitfall trap data illustrated the converse trend as more species in different class ranges were observed in recently cleared sites (cl 2 yrs) (Fig. 7b) the five years cleared sites species extending to more class ranges in comparison to 2 years cleared sites.

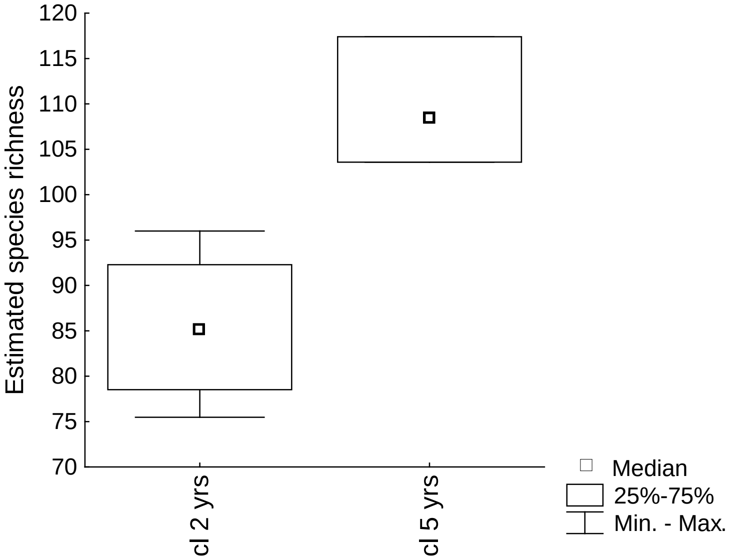
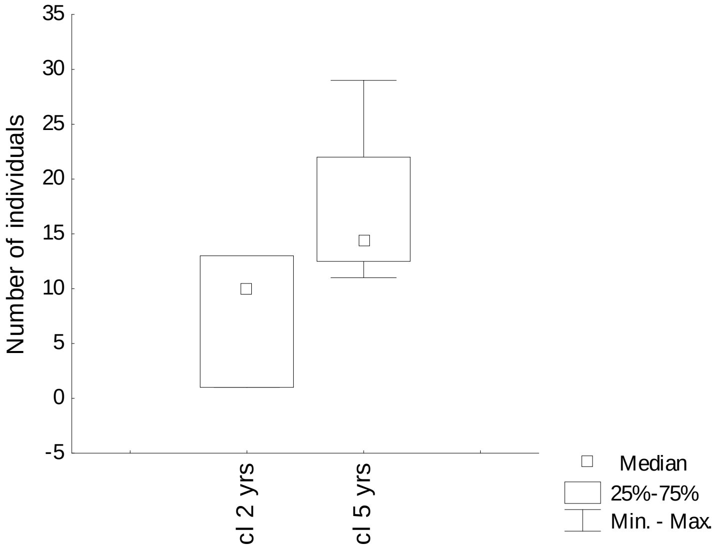
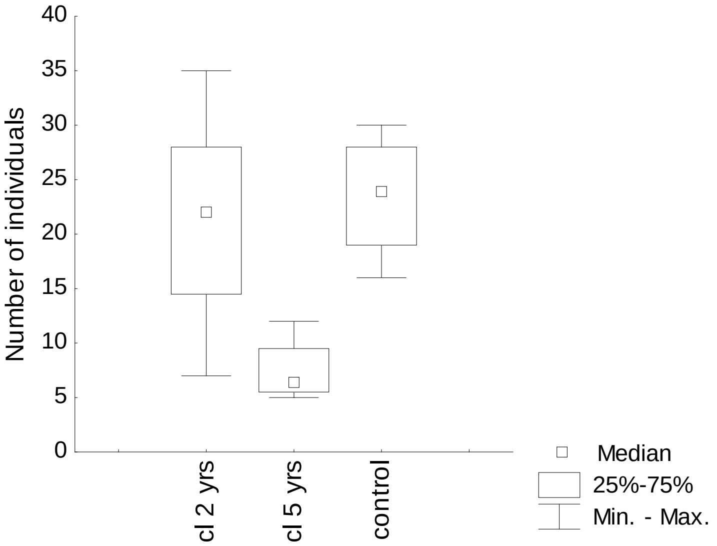


Fig. 5. Estimated species richness for the cleared sites for vegetation beating data (*U* = 0.000, z = -2. 1213, $P < 0.05$). Illustrating a higher estimated species richness for spiders inhabiting the *C. odorata* plant in the sites cleared for 5 years in comparison to sites that have been cleared 2 years ago.

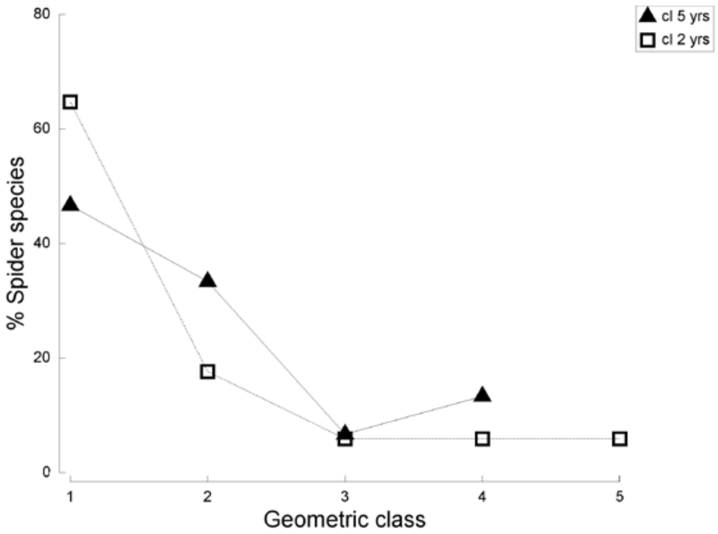


a)

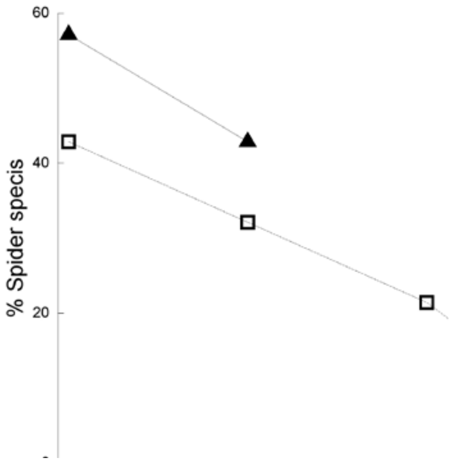


b)

Fig. 6. Abundance of spiders in the cleared sites **(a)** vegetation beating data showed that the spiders inhabiting *C. odorata* plants had the highest abundance in the site that was cleared 5 years ago and lowest in the site cleared 2 years ago ($U_{2,12} = 1.000$, $P > 0.05$) while the converse held true for pitfall trap data **(b)** with the highest abundance in the control and the lowest in the site cleared 5 years ago ($H_{2,16} = 7.639$, $P < 0.05$).



a)



b)

Fig. 7. The geometric class plot for the spider species illustrates a higher percentage contribution of rare species for the recently cleared sites (2 years) for both a) pitfall trap and b) vegetation beating data. However, pitfall trap data **(a)** illustrates that the site that has been recently cleared (2 years) has species extending over more class ranges as opposed to the sites cleared for 5 years. While vegetation beating data **(b)** illustrates the converse, with the 5 years cleared site extending to more class ranges in comparison to 2 years cleared sites.

Discussion

Chromolaena odorata invasions do alter native spider assemblage patterns as lower diversity and species richness was observed in invaded sites in comparison to uninvaded sites. Additionally, progressive invasion of *C. odorata* brings with it changes in native spider abundance, diversity (Table 1), assemblage patterns (Fig. 2) and estimated spider species richness (Figs 1a & 1b). The results show that *C. odorata* invasion alters and radically changes spider assemblages native to these habitats. Similarly, Greenwood, Dowd & Lake (2004) demonstrated distinct grouping between the native and the invaded sections, which indicated that the invasion had a strong overall effect on the species composition of terrestrial arthropods. The still relatively high species richness in newly invaded sites suggests that these sites have not been drastically altered or transformed by the invasion of *C. odorata*, and that there is still a high proportion of indigenous vegetation and thus a larger pool of spiders which invariably also inhabit the invasive plant. Harris *et al.* (2003) found that the extent to which native invertebrate communities are restructured may vary with the extent of change to the vegetation structure. As a result, a habitat may be able to accommodate a substantial number of alien plants before there is a negative impact on the insect consumers in that habitat (Tallamy 2004). The significantly higher species richness in newly invaded sites as opposed to the sites that have been invaded for longer durations demonstrates the negative impacts associated with cumulative invasion duration of *C. odorata* on spider communities (Fig. 1b). It has been found that the lower abundance and diversity of terrestrial arthropods in invaded sections than uninvaded sections is due to simpler habitat structure, lower plant diversity in invaded sections (Greenwood, O’Dowd &

Lake 2004) and there is a negative correlation of predator richness with decline in plant species richness (Knops *et al*. 1999; Longcore 2003).

On the positive side though, the effects of alien plant invasion on spider communities appear to be mostly reversible, as the clearing of *C. odorata* in this study resulted in previously invaded sites showing similar assemblages to the control sites after clearing (Fig. 4). The inconsistencies observed in the trends followed when assessing the data of the cleared sites from the different sampling methods denotes the immediate positive impact of clearing of *C. odorata* on native spider communities. Higher abundance is observed in recently cleared sites for pitfall trap data in comparison to sites that have been cleared for a longer duration (Fig. 6b). However, the converse trend is observed for the vegetation beating data which targeted spiders that inhabited *C. odorata*, with higher abundance observed in sites cleared for a longer duration (Fig. 6a). This suggests higher abundance was observed due to minimum residence time. Furthermore, supporting this trend was the pitfall trap data which highlighted the rapid positive impact of clearing *C. odorata*. Therefore, these results highlight the importance of clearing this invasive. Most importantly is that spider communities do re-establish after the weed has been cleared illustrating a high index of similarity to the control sites. Indeed, Gratton & Denno (2005) showed that removal of the invasive plant by herbicide application resulted in the rapid return of native plant species that are associated with an arthropod assemblage not distinguishable from that in uninvaded sites. Further supporting the importance and positive impact of *C. odorata* clearing is the higher diversity in cleared sites in comparison to sites that have been invaded for longer durations (Table 1).

Conclusion

Chromolaena odorata invasion resulted in reduction of numerically dominant spiders, changes in spider assemblage patterns, species richness and diversity. This is probably the result of disruption of food web interactions and flow of energy in invaded habitats (Tallamy 2004). This, in turn, may cause a trophic cascade and in turn may affect the density and diversity of insectivorous birds and other high order consumers (Levine *et al.* 2003; Greenwood, O'Dowd & Lake 2004). Also, invasive plant communities may not be functionally equivalent to the native plant communities in respect to arthropod food webs (Gratton & Denno 2005). Therefore, the return of spider communities to the cleared sites in comparable proportions to control sites not only restores the native arthropod diversity but also recreates the trophic structure (Gratton & Denno 2005). The findings of this study are consistent with the widely held view that vegetation structure is indeed of primary importance in determining the composition of spider assemblages (Wise 1993; Knops *et al.* 1999). They also support the observation that re-establishment of native vegetation in areas that have been altered or dominated by an invasive plant, can result in the restoration of the significant component of the biodiversity (Palmer, Ambrose & Poff 1997) making the effects of invasive alien plants reversible, even for sensitive indigenous taxa (Gratton & Denno 2005). Crucially, the variations in the impacts of different invasion durations of *C. odorata* found in this study show the great importance of incorporating the temporal variable in assessing impacts of invasive plants. Invasive species populations' sizes and environmental factors vary over time and the full effects of the invader might not be seen for a considerable time after the initial invasion, thus the chronic long-term effects of invasive plant species represent the actual outcomes of the species invasion (Strayer *et al* 2006).

Management applications

Alien clearing clearly is an essential and invaluable management tool. The small, but lingering differences between the native and the cleared habitats, however, may suggest that other features of the habitat may be affected by the invasion and clearing. There are a substantial number of programmes that aim to eradicate alien invasive plants, but, very little known about how biodiversity recovers after alien plant removal. Samways, Taylor & Tarboton (2005) showed that the removal of alien invasive plants benefits biodiversity with immediate effects, highlighting that effective management can be utilized to directly benefit irreplaceable biodiversity. Similarly, the clearing of *C. odorata* promotes the re-establishment of native spider assemblages. Therefore, clearing with follow up treatments as well as the prevention of invasion, of this notorious weed should be promoted, in order to conserve the native biota. The data can further be used to inform policy makers as to the effects of aliens and the value of restoration programmes for biodiversity.

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CHAPTER 4

Summary

Biological indicators measure components of the biota and are used to give general information about complex ecosystems in which they occur, playing key roles in conservation planning and management (Anderson 1999). This study illustrates the impact of habitat change or transformation by factors that are extrinsic to the habitats in question and the importance of spider responses in aiding management decisions. The spider responses illustrated indicate existence of environmental change and represent responses of other biota (McGeoch 2002).

The conclusions drawn from this study have important management implications for protected areas with grazing herbivores and occurrence of alien invasive plants. Grazed sites had the highest abundance, diversity and species richness. No grazing seems to have a negative impact on lower trophic levels, whereas grazing seems to result in favourable conditions for optimal abundance, diversity and species richness. Therefore, no grazing could have negative implications for other taxa in the food chain and may have cascading effects.

The higher abundance, diversity and species richness associated with grazed sites could be resulting from increased ground cover, greater variation with habitat structure (Samways & Kreuzinger 2001), increased plant diversity and enhanced soil/plant nutrient concentrations (Abenstraung-Traun *et al.* 1996). However, ungrazed sites in turn become more monotonous and provide less habitat diversity (Morris 1991) leading to lower abundance, diversity and species richness. However, the characteristic species for each grazing intensity level demonstrate the difficulty in making generalizations for management even for closely related species.

Furthermore, results from this study oppose the assumption that grazing lawns are a result of overgrazing and thus highly undesirable. This grassland type in comparison to tall bunch grassland displayed the highest spider diversity and species richness. Studies in the same exclosure plots illustrated more fauna and flora characteristic of the grazing lawns and not of any other grassland type. This further supports the conclusion that grazing lawns are steady state communities of their own and not a sub-set of any other grassland type. Therefore, veld management decisions that eradicate grazing lawns are negative for the park as the fauna and flora associated with this grassland type will be lost, leading to cascading effects.

Additionally, this study illustrated that habitat modification by invasion of invasive alien plant species has detrimental consequences for the endemic fauna. Extreme habitat modification may result from progressive invasion by alien invasive plants, which in turn affect the health and reproductive output of the system. The result of habitat modification or alteration results in a simpler habitat structure. Habitat heterogeneity has been demonstrated to be a primary determinant for spider diversity (Gibson *et al*. 1992) as opposed to abundance of prey (Wise 1993), because plant height and architecture drive spider colonization (Baudry & Asselin 1991).

The removal of alien invasive weeds results in returning a system to close approximation of its condition prior to disturbance, with both structure and function recreated (Palmer, Ambrose & Poff 1997). As was observed in this study, there were no significant differences in the assemblage structures from the control sites in comparison to cleared sites. Palmer, Ambrose & Poff (1997) pointed that assemblage patterns can be selected as endpoints to measure the ecological rehabilitation; thus the non-significant differences in assemblage patterns of the control *versus* cleared sites imply that the system is rehabilitating with clearing without further management intervention.

Plant species richness impacts other trophic levels and the reduction in abundance, diversity and species richness of spiders in invaded, overgrazed and undergrazed sites might have negative consequences for higher tropic levels (invertebrates and vertebrates) that include these invertebrates in their diets, i.e. insectivorous birds, amphibians, reptiles and mammals. This may result in trophic cascades' as trophic interactions are likely to be altered as reduction in numerically abundant spiders will likely have an effect on food-web interactions and the flow of energy in modified environments (Gratton & Denno 2005).

The conclusions drawn from this study have important management implications on managing grazer assemblages and highlighting the importance of eradicating alien plant invasions for the system to rehabilitate. This study further adds to the limited amount of information on the impact of grazing intensity levels, grassland types, short-term and long-term invasion and clearing of alien invasive plants on spider communities.

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APPENDICES

Appendix A. Number of species captured for the different grazing intensity levels (combined sampling data).

Family name	Scientific name	Intense grazing	Moderate grazing	No grazing
Ammoxenidae	*Ammoxenus amphalodes*	14	29	14
Araneidae	*Araniella* sp 1		3	3
	Araneus coccinella			1
	Araneus strupifer		1	4
	Cyclosa insulana		1	
	Hypsosinga lithyphantoides			1
	Hypsosinga sp 1			1
	Hypsosinga sp 2			1
	Hypsacantha sp 1			1
	Pararaneus cyrtoscapus	1		
	Pycnacatha tribulus	1		
Clubionidae	*Clubiona* sp 1	1	1	1
Corinnidae	*Corinnidae* sp 1			1
Ctenidae	*Anahita* sp 1		1	1
Gnaphosidae	*Aphantaulax inornata*	5		7
	Asemesthes ceresicola	4	3	2
	Camillina sp 1	3	1	1
	Setaphis sp 1	1		1
	Stenaelurillus sp 1		1	
	Zelotes oneili	1	1	
Idiopiidae	*Segregara pectinipalpis*		1	
Linyphiidae	*Linyphiidae* sp 1		3	
Lycosidae	*Evippomma squamulatum*	2	2	1
	Hogna sp 1	2	1	1
	Hippasa australis	1		
	Lycosa sp 2		1	1
	Lycosa sp1	1	2	
	Pardosa sp 1	1	1	1
	Pardosa sp 2	6	14	7
Miturgidae	*Cheiracanthium africanum*	3	6	3
Nemesiidae	*Hermacha* sp 1			2
Oecobiidae	*Oecobius* sp 1			1
Oxyopiidae	*Oxyopes jacksoni*			3
	Oxyopes longispinosa		2	
	Oxyopes pallidecoloratus		1	
	Oxyopes sp 1	19	6	2
Philodromidae	*Philodromus* sp 1		1	1
	Suemus punctatus		1	4
	Thanatus sp 1			1
	Thantus dorsolineatus	2	6	15
	Tibellus armatus	2	3	10
	Tibellus sp 1	1	6	11
Pholcidae	*Spermorphora* sp 1	1		

Appendix A continued…..

Family name	**Scientific name**	**Intense**	**Moderate grazing**	**No grazing**
Pisauridae	*Afropisaura rothiformis*	29	41	40
Pisauridae	*Afropisaura* sp 1		1	1
Prodidomidae	*Theuma foveolata*	1		
Salticidae	*Aelurillus* sp 1	3	2	2
	Evarcha sp 2	1	1	
	Evarcha sp *1*	9	8	11
	Hyllus sp 1			1
	Pellenes sp 1		2	
	Phlegra sp 1	1		
	Pellenes sp 2		1	
	Stenaelurillus sp 1		4	3
	Thyene sp 1	3	8	14
Sparassidae	*Olios* sp 1			1
Tetragnathidae	*Clitaetra irenae*		2	
	Leucauge sp 1		3	
Theridiidae	*Latrodectus geometricus*			1
	Phoroncidia			1
Thomisidae	*Heriaeus buffonii*	1		
	Monaeses pustulosus	1	5	2
	Monaeses fuscus	2	12	6
	Monaeses gibbus		2	
	Monaeses quadrituberculatus	3	12	1
	Oxytate argenteooculator		1	
	Runcinia affinis	2	4	
	Runcinia flavida	10	5	3
	Stiphropella gracilis	1		
	Synema nigrotibiale	1		2
	T marus sp 1	2		
	Thomisops granulatus		1	1
	Xyticus sp 1		1	
Zodariidae	*Caesetius* sp 1			1
	Cydrela sp 1	2	3	2
	Diores sequax		1	2
	Ranops caprivi	1		
	Totals	**145**	**219**	**199**

Appendix B. Number of species captured for the different grassland types (combined sampling data).

Family name	Scientific name	Grazing lawns	Tall Grass
Ammoxenidae	*Ammoxenus amphalodes*	16	
Araneidae	*Araniella* sp 1	1	2
	Araneus coccinella	1	
	Araneus strupifer	3	
	Hypsosinga sp 2	1	
	Hypsacantha sp 1	1	
	Pycnacatha tribulus	1	
Gnaphosidae	*Aphantaulax inornata*	1	2
	Asemesthes ceresicola	1	7
	Camillina sp 1		1
	Setaphis sp 1	1	1
	Zelotes oneili	1	
Linyphiidae	*Linyphiidae* sp 1	1	
Lycosidae	*Evippomma squamulatum*	4	
	Hogna sp 1		2
	Hippasa australis		1
	Lycosa sp 1	2	
	Pardosa sp 2	5	5
Miturgidae	*Cheiracanthium africanum*	3	
Nemesiidae	*Hermacha* sp 1	2	
Oecobiidae	*Oecobius* sp 1	1	
Oxyopiidae	*Oxyopes jacksoni*	1	1
	Oxyopes longispinosa	1	
	Oxyopes sp 1	1	
Philodromidae	*Philodromus* sp 1		1
	Suemus punctatus	1	1
	Thanatus sp 1	1	
	Thantus dorsolineatus	2	11
	Tibellus armatus		1
	Tibellus sp 1	5	2
Pisauridae	*Afropisaura rothiformis*	11	21
Prodidomidae	*Theuma fusca*	1	
	Evarcha sp 1	6	3
	Pellenes sp 1	1	
	Pellenes sp 2	1	
	Thyene sp 1	1	9
Sparassidae	*Olios* sp 1		1
Tetragnathidae	*Clitaetra irenae*	1	
	Leucage sp 1		2
Thomisidae	*Heriaeus buffonii*	1	
	Monaeses pustulosus	4	
	Monaeses fuscus	16	1
	Monaeses quadrituberculatus	3	
	Runcinia flavida	2	
	Stiphropella gracilis	1	

Appendix B continued

Family name	**Scientific name**	**Grazing lawns**	**Tall Grass**
Thomisidae	*Synema nigrotibiale*		1
	Thomisops granulatus	1	1
	Xyticus sp 1	1	
Zodariidae	*Caesetius* sp 1	1	
	Cydrela sp 1	1	
	Diores sequax	3	
	Ranops caprivi	1	
	Totals	**119**	**78**

Appendix C. Number of species per family in areas varying in altitude and rainfall gradients (combined sampling data).

Family name	Scientific name	Hluhluwe	IMfolozi
Ammoxenidae	*Ammoxenus amphalodes*		57
Araneidae	*Araniella* sp 1	6	
	Araneus coccinella		1
	Araneus strupifer	3	2
	Cyclosa insulana	1	
	Hypsosinga lithyphantoides	1	
	Hypsosinga sp 1	1	
	Hypsosinga sp 2	1	
	Hypsacantha sp 1	1	
	Pararaneus cyrtoscapus		1
	Pycnacatha tribulus	1	
Clubionidae	*Clubiona* sp 1		3
Corinnidae	*Corinnidae* sp 1	1	
Ctenidae	*Anahita* sp 1	1	1
Dictynidae	*Dictyna* sp 1		1
Gnaphosidae	*Aphantaulax inornata*	5	7
	Asemesthes ceresicola		9
	Camillina sp 1	4	1
	Setaphis sp 1	2	
	Zelotes oneili	1	1
Idiopiidae	*Segregara pectinipalpis*	1	
Linyphiidae	*Linyphiidae* sp 1	3	
Lycosidae	*Evippomma squamulatum*	1	4
	Hogna sp 1	4	
	Hippasa australis		1
	Lycosa sp 2		2
	Lycosa sp 1		3
	Pardosa sp 1	1	2
	Pardosa sp 2	13	14
Miturgidae	*Cheiracanthium africanum*	3	9
Nemesiidae	*Hermacha* sp 1		2
Oecobiidae	*Oecobius* sp 1	1	
Oxyopiidae	*Oxyopes jacksoni*	1	2
	Oxyopes longispinosa	1	1
	Oxyopes pallidecoloratus		1
	Oxyopes sp 1		27
Philodromidae	*Philodromus* sp 1	1	1
	Suemus punctatus	2	3
	Thanatus sp 1	1	
	Thantus dorsolineatus	2	21
	Tibellus armatus		15
	Tibellus sp 1	6	12
Pholcidae	*Spermorphora* sp 1	1	
Pisauridae	*Afropisaura rothiformis*	15	95

Appendix C continued…..

Family name	**Scientific name**	**Hluhluwe**	**IMfolozi**
Pisauridae	*Afropisaura* sp 1		2
Prodidomidae	*Theuma foveolata*	1	
	Theuma fusca	1	2
Salticidae	*Aelurillus* sp 1	5	2
	Evarcha sp 2		2
	Evarcha sp 1	6	22
	Hyllus sp 1		1
	Pellenes sp 1	2	
	Pellenes sp 2	1	
	Phlegra sp 1	1	
	Stenaelurillus sp 1	1	7
	Thyene sp 1	3	22
Sparassidae	*Olios* sp 1	1	
Tetragnathidae	*Clitaetra irenae*	2	
	Leucage sp 1	3	
Theridiidae	*Latrodectus geometricus*		1
	Phoroncidia		1
Thomisidae	*Heriaeus buffonii*		1
	Monaeses pustulosus	6	2
	Monaeses fuscus	15	5
	Monaeses gibbus	2	
	Monaeses quadrituberculatus	6	10
	Oxytate argenteooculator		1
	Runcinia affinis	5	1
	Runcinia flavida	2	16
	Stiphropella gracilis		1
	Synema nigrotibiale		3
	T marus sp 1		2
	Thomisops granulatus	2	
	Xyticus sp 1	1	
Zodariidae	*Caesetius* sp 1		1
	Cydrela sp 1	2	5
	Diores sequax	3	
	Ranops caprivi	1	
	Totals	**158**	**409**

APPENDIX D. Number of species per family captured for sites differing in *c. odorata* invasion and clearing durations sampled by pitfall traps and vegetation beating in Hluhluwe-iMfolozi Park.

Family	**Species**	**Guild**	**10 yrs**	**20 yrs**	**cl 2 yrs**	**cl 5 yrs**	**control**	**< 2 yrs**
Araneidae	*Araniella* sp 1	OWB	2	2		4		2
	Araneus holzapfelae	OWB				1		1
	Araneus sp 1	OWB	1	1	3	2		
	Chorizopes sp 1	OWB				1		
	Cyphalonotus larvatus	OWB				2		2
	Hypsosinga lithyphantoides	OWB		1				
	Hypsosinga sp 2	OWB	1					
	Nemoscolus vigintipunctatus	OWB				1		
	Neoscona blondeli	OWB	3	1			1	3
	Neoscona subfusca	OWB	1	2		1	1	2
	Pararaneus cyrtoscapus	OWB						1
	Singa sp 2	OWB						1
Capaniidae	*Caponia* sp 1	GD	1					
Clubionidae	*Clubiona* sp 1	PD	6	8	3	5		5
Corinnidae	*Corinnidae* sp 1	GD	1	1		2	2	1
	Corinnidae sp 2	GD	1	1	2	1	1	1
	Corinnidae sp 3	GD		1				
	Corinnidae sp 4	GD						1
Ctenidae	*Anahita* sp.1	GD	5	5	7	3	5	3
Cyrtaucheniidae	*Homostola sp 1*	BGD				1	1	
Deinopidae	*Menneus camelus*	OWB(WB)				1		
Gnaphosidae	*Aphantaulax inornata*	GD		1				
	Asemesthes ceresicola	GD	2					4
	Camillina procurva	GD	2	1	6	2	1	4
	Setaphis sp 1	GD	4	2				1
	Zelotes oneili	GD		1	1		1	2
	Zelotes reduncus	GD		1			1	

Appendix D continued.....

Family	**Species**	**Guild**	**10 yrs**	**20 yrs**	**cl 2 yrs**	**cl 5 yrs**	**control**	**< 2 yrs**
	Zelotes tuckeri	GD		5	1		2	3
	Zelotes ungulus	GD	1	1	2		1	4
Idiopidae	*Segregara pectinipalpis*	BGD		1				
Linyphiidae	*Linyphiidae* sp 1	SWB	2	2	2	1	2	3
Lycosidae	*Evipomma squamulatum*	GD			1			2
	Hippasa australis	FWB	1		1		2	
	Hogna sp 1	GD	20	8	17	5	23	24
	Lycosa sp 1	GD				1	1	3
	Minicosa neptuna	GD	1	1				
	Pardosa crassipalpis	GD						1
	Pardosa foveolata	GD					1	
	Pardosa sp 1	GD	9	16	34	8	25	26
	Pardosa sp 2	GD			2	1	1	
	Trabea sp 1	GD				3	3	1
Miturgidae	*Cheiracanthium africanum*	PD			1			1
	Cheiracanthium vansoni	PD	8	3	3	4	1	7
	Cheiramiona paradisus	PD	1		1	1		4
Nemesiidae	*Hermacha* sp 1	BGD	2		1		1	4
	Hermacha sp 2	BGD						1
Oxyopidae	*Hamataliwa* sp 1	PD						2
	Oxyopes pallidecoloratus	PD	1	2	1		1	
Palpimanidae	*Palpimanus* sp 1	GD	1					
Philodromidae	*Philodromus* sp 1	PD		3		1	1	
	Philodromous sp 2	PD		1				
	Suemus punctatus	PD		2			1	2
Pisauridae	*Afropisaura rothiformis*	PD	1	1				
	Chiasmopes sp 1	PD	1					
	Maypacius bilineatus	SWB						1
Salticidae	*Baryphas ahenus*	PD	1					
Salticidae	*Evarcha dotata*	PD	1					1

Appendix D continued.....

Family	**Species**	**Guild**	**10 yrs**	**20 yrs**	**cl 2 yrs**	**cl 5 yrs**	**control**	**< 2 yrs**
	Evarcha sp 1	PD	10	5	1	6	1	1
	Heliophanus sp 1	PD	1		1			2
	Hispo inermis	PD	1					1
	Hyllus argyrotoxus	PD	3	1		2		1
	Natta horizontalis	GD	1				1	
	Pellenes sp 1	PD					1	1
	Phlegra sp 1	GD					1	
	Stenaelurillus sp 1	GD	1			1	1	3
	Thyene coccineovittatus	PD						1
	Thyene inflata	PD	30	13	2	13		11
	Thyene natalii	PD	1	1		3		2
	Thyene sp. 4	PD	1	1				2
	Thyenula aurantiaca	PD					1	
Sparassidae	*Olios correvoni*	PD	9	5		3		1
	Olios sp 2	PD	1	2		2		
	Olios sp 3	PD				1		2
Theraphosidae	*Harpactirella* sp 1	BGD			1	1		1
Theridiidae	*Dipoena* sp.	GFWB	3			2		
	Euryopis sp 1	GD		1		1		
	Euryopis sp 2	GD						1
	Latrodectus geometricus	GFWB	1					
	Steatoda sp 1	GFWB						1
	Theridion sp. 2	GFWD						1
	Theridion sp. 3	GFWD						1
	Theridion sp. 1	GFWB	3	1	1	3	2	
Thomisidae	*Ansiae tuckeri*	PD			1			
	Diaea puncta	PD	9		5	4		11
	Heriaeus buffoni	PD		2				
Thomisidae	*Oxytate argenteooculata*	PD	1	3	1	1		
	Pherecydes sp. 1	PD						1
	Synema nigrotibiale	PD	3	2		1		1

<u>Appendix D</u> continued.....

Family	**Species**	**Guild**	**10 yrs**	**20 yrs**	**cl 2 yrs**	**cl 5 yrs**	**control**	**< 2 yrs**
	Tmarus cameliformis	PD	5	9	1	2		2
	T marus sp 2	PD	1	3				
	Thomisops pupa	PD	9	4	1	6		3
	Thomisus blandus	PD				1		
	Thomisus daradioides	PD						2
	Thomisus stenningi	PD						1
	Thomisus scrupeus	PD	1					
	Xysticus sp 1	GD	1					
Uloboridae	*Miagrammopes* sp 1	OWB					1	
Zodariidae	*Caesetius* sp 1	GD	2	2	1	1		
	Capheris sp 1	GD			1	1	1	
	Cydrela sp 1	GD	2	18	2	3	7	2
	Diores sequax	GD				1		1
	TOTALS		**181**	**148**	**108**	**111**	**97**	**180**

GD – ground dweller; PD – plant dweller; BGD – burrow ground dweller; OWB- orb-web; SHWB – sheet-web; FWB – funnel web; GFWB – gumfoot-web.