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Arthropod assemblages in a savanna invaded by *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa

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Arthropod assemblages in a savanna invaded by *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa

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SUMMARY

Invasive alien species are considered the second greatest threat to global biodiversity after habitat loss. South Africa is not immune from such threats and it is estimated that 10 million ha (8.28 %) of land has been invaded to some extent by invasive alien species. Although South Africa has been invaded by several taxa, it is the effect of invasive trees and shrubs that has been environmentally and economically most damaging. The concerns raised due to the effects of biological invasion are not only restricted to off-reserve areas, but also protected areas where invasive alien organisms often pose a greater threat than habitat loss. Kruger National Park (KNP), South Africa's flagship conservation area has been invaded by numerous plant taxa. The most damaging of these is *Opuntia stricta* (Cactaceae) and current sources estimate that the weed has invaded approximately 35 000 ha of conserved land, despite the initiation of a biological control programme against it. However, little is known about the effect of *O. stricta* on biodiversity in the KNP despite the large number of resources allocated to its eradication, including a successful biological control programme against it. In this study, I investigated the effect of *O. stricta* infestation on beetle (Order Coleoptera) and spider (Order Araneae) assemblages across four treatments of varying *O. stricta* infestation levels (heavy infestation, medium infestation, surrounded sites and pristine sites). Species characteristic of each treatment (indicator species) were identified using the indicator method. In addition, spiders were collected to gauge the effectiveness of three collecting methods (pitfall traps, leaf litter sifting and active searching) in a savanna characterized by *O. stricta* invasion. One hundred and thirty one spider species (1050 individuals) and 72 beetle species (2162 individuals) were collected in the treatments. I found no significant differences in species richness, species density and species assemblages for both beetles and spiders across the treatments. In addition, no beetle or spider species were found to be characteristic indicator species for a given treatment, which further indicates that arthropod assemblages are similar when compared across treatments. These results indicate that *O. stricta* does not appear to have a significant effect on beetle and spider assemblages at its current infestation level, possibly because of the similarity in vegetation structure across the treatments. Regarding spiders, different collecting methods captured different species and only 17 % of the species were shared, indicating that the methods complement each other. Therefore, in order to sample the spider community, all three methods should be employed. Of the 131 spider species collected, 54 species (41 %) are new records for the KNP. In light of the results, it is suggested that KNP's successful biological control programme has played an important role in reducing the extent of the *O. stricta* infestation and should be continued to further mitigate the impacts of *O. stricta*.

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DISCLAIMER

The two experimental chapters contained in this thesis have been prepared for submission to different scientific journals. As a result, content overlap may occur in order to secure publication.

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CHAPTER 1

GENERAL INTRODUCTION

Introduction

Biological invasions are the second greatest threat to biodiversity after habitat loss (Mooney & Hobbs 2000). Aside from the impacts on biodiversity, invaders also threaten agriculture, forestry, ecosystem services and human health (Richardson & van Wilgen 2004). Oceanic islands are particularly susceptible to invasion by non-native species and Hawaii and New Zealand are two well-studied examples (Loope & Mueller-Dombois 1989). The Hawaiian island chain contains a large number of endemic species, but over 70 % of endemic land bird and snail species have been lost primarily due to mammalian invasions (Steadman 1995). In New Zealand, for most of the threatened animal and plant species, invasive species now pose the greatest remaining threat to their continued survival. Although the greatest threat here is arguably from introduced mammals, many invasive plants have the ability to alter native ecosystems over a long period of time (Clout & Lowe 2000). Similarly, Chile is plagued with a large number of invasive plants with a total number of 690 alien species contained in 73 families and 37 genera that have become naturalized in continental Chile since the colonial period (Arroyo *et al.* 2000). Globally, the economic impacts of alien invasive species on ecosystems and biodiversity are significant, with the total cost in the order of tens of billions of US$ each year (Pimental *et al.* 2005). Scalera (2009) suggests that the European Commission (EC) has spent over €132 million on alien invasive species in the past 15 years. While in South Africa, government's expenditure between 1995 and 2000 on the control and eradication of invasive plants amounted to over R100 million (van Wilgen *et al.* 2001).

Biological invasions in South Africa

South Africa, like many other countries, is under threat from biological invasions and current sources estimate that about 10 million ha (8.28 %) of the country have been invaded to some degree by a wide range of plant and animal species (Le Maitre *et al.* 2000). If this area is condensed to adjust the cover to 100 %, then the area is equivalent to

1.7 million ha (1.39 %) under invasion and is larger than the area of Gauteng Province (Le Maitre *et al.* 2000). Current sources indicate that South Africa contains 1226 plant species that are not native to the country (Richardson *et al.* 2005). Of these species, 198 species are declared weeds and invaders according to the Conservation of Agriculture Resources Act, Act 43 of 1983, amended in 2001 (Henderson 2001). Invasive alien organisms from most taxa have negatively affected ecosystems in South Africa, it is however the effect of invasive trees and shrubs that have had the most impact ecologically and economically (Richardson *et al.* 1997). The species rich Fynbos vegetation of the Cape Floristic Region is particularly susceptible to the impacts of invasive plants and currently has the highest levels of alien plant infestations when compared to any other biome (van Wilgen *et al.* 2008). At present, human land use and invasive alien plants have transformed nearly a third of the area of The Cape Floristic Region (Latimer et al. 2004). Fire-tolerant woody species from Mediterranean-type ecosystems are particularly problematic as they are pre-adapted to local conditions and are able to spread and form dense stands following fires (Richardson *et al.* 1996).

In an effort to prioritize alien plant species for management action, Nel *et al.* (2004) identified 117 major invaders that are well established and have substantial impact on natural and semi-natural ecosystems and 84 emerging invaders that have less influence on natural ecosystems. The emerging invaders do however have the attributes and potentially suitable habitat that could result in increased range and consequences in the next few decades. Of these 117 major invaders, black wattle (*Acacia mearnsii*), white and grey poplars (*Populus alba/canescens*) and mesquite (*Prosopis glandulosa*) are considered to be the most troublesome and fall into the "very wide-spread-abundant" category (Nel *et al.* 2004). The impacts of these invasive plants (and others) in South Africa vary immensely and range from impacts on ecosystem functioning in the delivery of goods and services (van Wilgen *et al.* 2008), impacts on surface water resources (Le Maitre *et al.* 2000; 2002; Görgens & van Wilgen 2004), impacts on rivers and catchment areas (van Wilgen & Rouget 2007), increase in biomass leading to increased fuel loads (van Wilgen & Richardson 1985) and impacts on biodiversity (Steenkamp & Chown 1996; French & Major 2001; Samways & Taylor 2004; Coetzee *et al.* 2007). In response, the Working for Water Programme was launched in 1995 by the Department of Water

Affairs and Forestry. The programme aims to remove water-demanding alien invasive plants from waterways and catchment areas, thereby creating jobs for up to 35 000 previously unemployed people and reducing the need for future dams (van Wilgen *et al.* 1998). It is estimated that 1.7 million ha of land containing about 15 woody invaders will be cleared by 2015 (van Wilgen *et al.* 1998), significantly contributing to reducing the impacts of these invaders.

Biological invasions in Kruger National Park

The concerns raised because of biological invasions are by no means restricted to off-reserve areas, or the matrix in which protected areas are embedded. In protected areas, the greatest threat to biodiversity is usually not habitat loss, but invasive species. As biologists and conservation managers, we should be deeply concerned about managing the world's protected areas in a responsible and sustainable manner seeing that, except for Antarctica, there is almost no reserve in the world known to be without some introduced species (Usher 1988). For example, a study by Lonsdale (1999) indicated that *c*. 8 % of the total plant richness of protected areas across the globe consists of alien plants. With biological invasions being a major threat to the preservation of modern biodiversity (Vitousek 1990; Gordon 1998), the occurrence of alien species in protected areas poses a serious threat to one of the cornerstone activities of most conservation bodies, namely to maintain formally protected areas. Human population densities are strongly correlated with anthropogenic activities (Harcourt *et al.* 2001) and both the former (McKinney 2001) and the latter being correlated with biological invasions (Le Maitre *et al.* 2004). Designated reserves (especially in Africa) are under increasing pressure as high human population densities often surround them (Harcourt *et al.* 2001; Parks & Harcourt 2002; Chown *et al*. 2003; Wittemeyer *et al*. 2008).

Kruger National Park (KNP), South Africa's flagship conservation area, has been invaded by numerous taxa, especially plants (Freitag-Ronaldson & Foxcroft 2003). Management authorities first noticed the presence of alien plants in the park during 1937 and since then the number of such invasive species and the scale of their impacts have increased tremendously (Foxcroft & Richardson 2003). The KNP's mission is "to maintain biodiversity in all its natural facets and fluxes and to provide human benefits in keeping with the mission of the South African National Parks in a manner which detracts as little as possible from the wilderness qualities of the KNP" (Sanparks 2003). However, the impacts of alien invasive species represent a major obstacle in attaining the KNP's goals of biodiversity maintenance. The current alien impact objective is stated as follows: *"To anticipate, prevent entry, eradicate or minimize the influence of non-indigenous organisms so as to maintain the integrity of native biodiversity"* (Foxcroft & Freitag-Ronaldson 2004). Invasive alien species are the greatest threat to biodiversity in the KNP ahead of traditional threats such as fragmentation and poaching (Foxcroft & Freitag-Ronaldson 2004). Currently, 370 alien plant taxa have been recorded in the KNP (Foxcroft *et al.* 2003). *Opuntia stricta* (Haworth) Haworth (Cactaceae) is the most widespread of these invasive plants and it is estimated that the plant has invaded 35 000 ha of conserved land (Foxcroft *et al.* 2007). *Opuntia stricta* has been classed as a transformer species, which is an invasive species that changes the character, condition, form or nature of ecosystems over a substantial area (Richardson *et al.* 2000).

The KNP management system is based on a framework of thresholds of potential concern (TPC) and invasive alien species have been included in this system (Foxcroft & Richardson 2003). These thresholds represent the upper and lower limits of acceptable change in ecosystem structure, function and composition over time and at a specified spatial scale (Foxcroft & Richardson 2003). The threshold is breached when one or more of these limits are exceeded. Once exceeded, appropriate management interventions are implemented. Regular monitoring is required to establish if a TPC has been surpassed or breached (Foxcroft & Downey 2008). In many instances the data to support these thresholds are limited and the TPCs are articulated as hypotheses, requiring testing and refinement (Biggs & Rogers 2003; Foxcroft 2004). The alien invasive species TPCs are divided into three distinct management responses or levels relating to the invasion process or pathway (Foxcroft & Downey 2008) and are discussed further:

1. The first level TPC targets new invasions or incursions into KNP. This TPC is breached by either an external threat (i.e. a species on the border of KNP, which has the potential to invade within 12 months) or the first occurrence of an invasive species in the KNP (Foxcroft & Downey 2008).

2. The second level TPC targets increases in distribution of invasive alien species already in the KNP. KNP has been divided into grid cells (the size has not been confirmed) which are routinely searched and changes in distribution can therefore be identified. A breach occurs once an alien species already present in KNP is recorded in a new cell and the new record is not in a cell adjoining the species current distribution, or new cells represent a greater than 5% increase in the number of cells occupied previously, despite active intervention (Foxcroft & Downey 2008).
3. The third level TPC targets increases in the density of an invasive alien species in KNP. This TPC is stated as a hypothesis and is not yet operational, due to the lack of data and cost-efficient monitoring options to detect such thresholds (Foxcroft & Downey 2008). Irrespective, this TPC will use a range of defined densities (being scattered, low, medium, and high) to determine breaches, as any increase in density of an alien plant can be used as a surrogate measure for an increase in biodiversity impacts (Foxcroft & Downey 2008).

The next step would be the development of TPCs that highlight the point at which invasive alien species present a measurable threat to biodiversity, composition or structure of an area (Foxcroft & Downey 2008). According to Foxcroft & Downey (2008) Level 3 TPCs require further work in the form of 1) developing a monitoring programme that provides the necessary data to evaluate those TPCs and 2) to be able to relate particular abundances to negative impacts on biodiversity. Once this information is available, KNP management will be able to develop new 'biodiversity impact' or biodiversity thresholds of potential concern (bTPCs) that either directly or through the use of appropriate surrogates address the issue of the negative impacts of alien species on biodiversity (Foxcroft 2008).

Bioindicators

The ecological impacts of invasive plants is difficult to define and measure (Parker *et al.* 1999) and consequently a major challenge in the field of invasion biology is to quantify these impacts and how they vary for different species in different geographical areas (van Wilgen 2004). According to Parker *et al.* (1999), the estimate of an invader's impact on native species may depend on the spatial and temporal scale of the study. Similarly, responses of native species to invasion are also expected to vary depending on spatial and temporal scales. Furthermore, the composite community measures (such as species richness, evenness and various indices of diversity) commonly used to measure the effects of invaders on communities often ignore much information and a more substantial multivariate analysis would be more informative (Parker *et al.* 1999). Capturing the entire, multidimensional response of a community is often not feasible, therefore searching for bioindicators whose presence and abundance may detect changes occurring at the whole community or ecosystem level is much more feasible (Parker *et al.* 1999).

Invertebrates contribute to the bulk of the earth's species diversity (Wilson 1987) and regulate many important processes (such as pollination and natural regulation of plant pests) fundamental to ecosystem functioning (Zhang *et al.* 2007). Beetles (Order: Coleoptera) and spiders (Order: Araneae) have been shown to be good indicators of habitat quality and change in several studies (van Rensburg *et al.* 1999; Pétillon *et al.* 2005; Pearce & Venier 2006) and could be useful taxa to use in order to quantify the effects of invasive plants on biodiversity. Bioindicators are classified into three categories: biodiversity, environmental and ecological indicators (McGeoch 1998). A biodiversity indicator indicates the presence of a set of other species and provides a descriptive function (Noss 1990). Environmental indicators show change in the state of the abiotic environment directly and ecological indicators demonstrate the effects of environmental change on the biotic systems including species, communities and ecosystems (McGeoch 1998, Pearce & Venier 2006). The characteristics of bioindicators depend on the specific goals of the type of monitoring in question. These goals usually include: 1) they must be feasible and cost effective to sample, 2) be easily and readily identifiable 3) must have a short generation time 4) must play a key role in the functioning of the community and 5) must respond to disturbance in a consistent matter (Parker *et al.* 1999; Pearce & Venier 2006).

Study species

Opuntia stricta (Haworth) Haworth (Cactaceae) is a perennial succulent shrub that is native to North and Central America. Fleshy fruits are produced on the modified succulent stems called cladodes. The species is well established as an invasive weed in Portugal (Monteiro *et al.* 2005), Australia (Hosking *et al.* 1988), Spain (Vilá *et al.* 2003) and South Africa (Nel *et al.* 2004). According to records from the Pretoria National Herbarium, *O. stricta* was first recorded in South Africa in 1937 (Henderson 2006) and was first recorded in the Kruger National Park (KNP) in 1953 as an ornamental plant in the Skukuza village (Lotter & Hoffmann 1998). The infestation in KNP is centred around Skukuza and radiates out approximately 20 km in all directions (Foxcroft *et al.* 2007). Of the 35 000 ha invaded, 2000 ha are considered to be densely covered, 17 000 ha as moderately covered and the rest as relatively sparse (Lotter 1996). *Opuntia stricta* seeds are dispersed in the Park predominantly by the African Elephant (*Loxodonta africana*) and the Chacma Baboon (*Papio ursinus*) (Foxcroft *et al.* 2004). Other possible dispersal routes include floodwaters, rivers, birds (Lotter & Hoffmann, 1998) and in parts of Mexico, small mammals such as mice are reported dispersal vectors (Vilà & Gimeno 2003). *Opuntia stricta* has many traits that contribute to its invasive nature, including its prolific seed production and vegetative propagation by means of ramets (i.e. fragments containing one or more cladodes) (Foxcroft *et al.* 2004). Other invasive traits include the ability to compete strongly with desirable species for growth resources, insignificant herbivory of vegetative parts (Wells *et al.* 1986) and a high stress tolerance to salinity and drought (Luo & Nobel 1993).

Several attempts have been made to control the spread of *O. stricta* in the Park. In 1985 the use of herbicides was launched, but was not wholly successful on its own as the plant regenerates after a few years from seeds, which are stored in the soil and can remain dormant for long periods of time (Reinhardt *et al.* 1999). In addition, smaller plants are often overlooked in spraying operations, eventually grow to maturity, and subsequently spread (Foxcroft *et al.,* 2004). In 1988, the biological control programme began with the introduction of the phycitid moth *Cactoblastis cactorum* (Lepidoptera: Pyralidae). The moth has played a vital role in curtailing regrowth of *O. stricta* and extending the time that plants take to reach sexual maturity (Hoffmann *et al.* 1998a, 1998b). Biological control of *O. stricta* in KNP was increased with the release of the cochineal insect *Dactylopius opuntiae* (Homoptera: Dactylopiidae) in 1997 (Foxcroft & Hoffmann 2003). Initially, large dense clumps of *O. stricta* were destroyed within 18 months; however, *D. opuntiae* populations declined rapidly in 2000-2001 due to the high rainfall experienced (Foxcroft & Hoffmann 2003). The combined effect of both *C. cactorum* and *D. opuntiae* has not been able to prevent the spread of *O. stricta.* It has however managed to curtail the densification and the long-range dispersal of the plant (Hoffmann *et al.* 1998a; 1998b). With the success of the cochineal insect on target weeds in areas of below-average rainfall (Moran *et al.* 1997), it is expected that the same will happen in the next dry period in KNP (Foxcroft & Hoffmann 2003).

Study area

This study was conducted in the Skukuza region of the KNP, which is situated in the Limpopo and Mpumalanga Provinces in the eastern part of South Africa and is bordered on its entire eastern side by Mozambique (Fig.1). High-density communal areas, private and provincial game reserves border KNP to the west. The KNP extends 360 km from north to south, has an average width of approximately 60 km and covers a surface area of 20 000 km^2, making it one of the world's largest protected areas (Mabunda *et al.* 2003). The topography of the KNP varies from plains with low relief, slightly and moderately undulating plains, low mountains and hills to extremely irregular incised areas (Venter *et al.* 2003). Seven major perennial river systems flow into the KNP in a west-east direction originating in the highlands to the west and drain a combined area of about 88 600 km^2 (Foxcroft & Richardson 2003). All these rivers flow through the Park into Mozambique and act as conduits for dispersal for many invasive species (Foxcroft & Richardson 2003).

The KNP falls into the savanna biome, which is defined as having a discontinuous overstory of woody plants and an herbaceous layer dominated by C_4 grasses (Scholes 1997). Vegetation within the KNP has been classified into 35 landscape types (Gertenbach 1983) which forms the basis for dividing the park into manageable sectors (Foxcroft & Richardson 2003). The vegetation in all but the wettest parts of Kruger is defined as semi-arid to arid wooded savanna (Mabunda *et al.* 2003). KNP falls within two climatic zones as defined by the South African Weather Service (Weather Bureau 1986). The lowveld bushveld zone constitutes the south and central portion of the Park and is characterized by an average rainfall of 500 – 700 mm/year. The northern portion falls into the northern arid bushveld zone with an average rainfall of 300 – 500 mm/year (Venter *et al.* 2003). The underlying geology of Kruger is roughly a west-east split, with granitic rocks in the west and basaltic rocks in the east. A thin north-south strip of sedimentary rocks separates the granitic and basaltic rock formations (Venter *et al.* 2003).

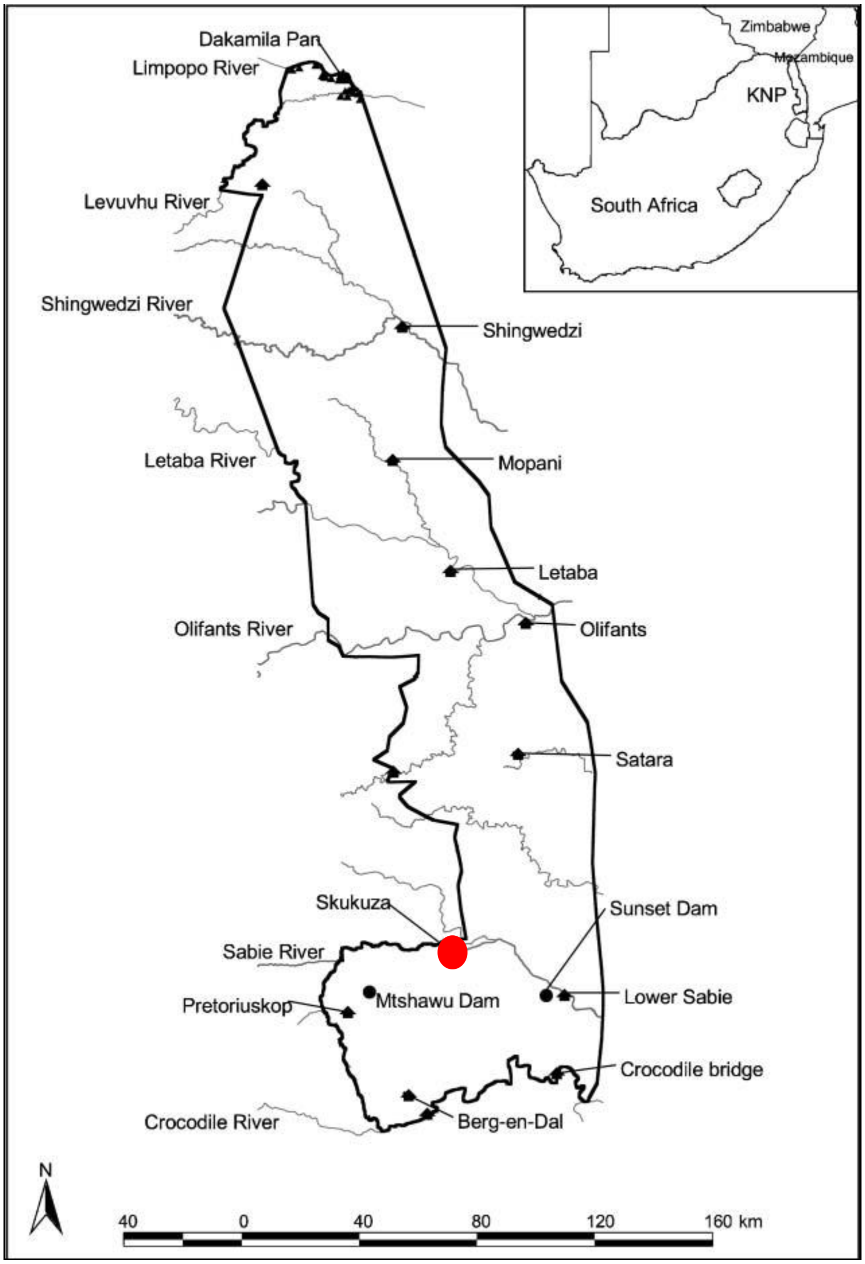

Fig.1. Map of the Kruger National Park showing the location of the study site at Skukuza. The inset shows the location of KNP in South Africa. Map taken from Foxcroft & Freitag-Ronaldson (2007).

The *O. stricta* invaded area encompasses an area of approximately 35 000 ha and has decreased significantly since the introduction of the two biocontrol agents (Foxcroft pers. comm.). At present, the *O. stricta* infestation is discontinuous and scattered and the largest of the patches is approximately 120 m^2 (Fig.2). The remaining patches have decreased in height, (from 5 m to now currently 2 m) and in area (Lotter & Hoffmann 1998).

The study site is characterized by native woody species such as *Dichrostachys cinerea* Wight & Arn. (Mimosaceae), *Spirostachys africana* Sonder (Euphobiaceae) and *Grewia bicolor* Juss. (Malvaceae). *Panicum maximum* Jacq. (Poaceae), *Pogonarthria squarrosa* (Roem. & Schult.) Pilg. (Poaceae) and *Aristida congesta* Roem. & Schult. (Poaceae) are grasses that dominate the understory vegetation.

Fig. 1. Patchy nature of the *Opuntia stricta* invaded site in the Skukuza region of the Kruger National Park.

Objectives and aims

The initial objective of this study was to gain a better understanding of the effects of *O. stricta* on beetle and spider assemblages in the KNP. Beetles and spiders were selected as focal taxa for this study for two main reasons. Beetles (especially dung beetles; Coleoptera: Scarabaeidae) are systematically well known in southern Africa (Davis 1997) and are known to play important roles in ecosystem functioning in tropical

African savannas (Hanski & Cambefort 1991). Spiders constitute a highly diverse group and their position in the trophic level and their mobility suggests that they also play an important part in ecosystem functioning (Wise 1995). Little is known about the effects of *O. stricta* on arthropod assemblages within KNP and to my knowledge; no other studies have investigated this issue. Although several other arthropod taxa were collected during the study (including ants and millipedes), they were not incorporated into the study due to time constraints.

Following from the objective, the aims of the study are as follows:

- Aim 1a: Assess the impacts of *O. stricta* on beetle and spider assemblages in KNP.
- Aim 1b: Identify beetle and spider species characteristic of each *O. stricta* infestation level.

- Aim 2a: Assess the degree to which different methods (pitfall trapping, active searching and leaf litter sifting) often used to capture spider species complement each other in a highly transformed savanna habitat in the KNP
- Aim 2b: Evaluate these methods in terms of effort required to obtain representative spider samples.

Expected outcomes

Consensus within the literature suggests that invasive alien plants can have negative effects on biodiversity within South Africa (Coetzee *et al.* 2007; Mgobozi *et al.* 2008). For example, Mgobozi *et al.* (2008) found that stands of invasive *Chromolaena odorata* in Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal in South Africa had lower species diversity and species richness of spider assemblages. Similarly, Coetzee *et al.* (2007) found that invasion by *Acacia dealbata* in grasslands in the Maloti-Drankensberg in South Africa reduced species richness and abundance of coleopteran assemblages. Changes in plant architecture caused by the introduction of invasive alien plants are probably the major cause of reductions in species richness and abundance (e.g. Coetzee *et al.* 2007; Mgobozi *et al.* 2008). However, a recent study by Pearson (2009) has shown that invasion by a perennial forb, *Centaurea maculosa*, in a North American grassland, increased spider species abundance when compared to uninvaded sites.

With these results in mind, I expected that *O. stricta* would have an effect on both spider and beetle assemblages, in that species richness and abundance of both arthropod groups would be significantly higher in pristine patches when compared with *O. stricta* invaded areas. Furthermore, I expected that a number of spider and beetle species would be indicators of each *O. stricta* infestation level.

Numerous studies have suggested different methodologies for collecting spiders in ecosystems around the world. However, these studies have generally focused on sampling techniques for spiders in tropical forests (Coddington *et al.* 1991; Coddington *et al.* 1996), montane forests (Sørensen *et al.* 2002) and Heathland vegetation in Australia (Churchill & Arthur 1999). Sampling methodologies are generally lacking in savanna environments with relatively few studies conducted (Whitmore *et al.* 2002; Dippenaar-Schoeman & Leroy 2003). A study conducted by Whitmore *et al.* (2002), found that more than one trapping method was required to sample the spider community in a savanna environment adequately. Whitmore *et al*. (2002) further suggests that surveys including sweeping, beating and active searching would be ideal for a representative sample. However, no other studies have focused on the effectiveness of sampling techniques for collecting spiders in a savanna that has been transformed by an alien invasive plant. The physical transformation of the savanna environment by *O. stricta* is distinctly noticeable, *O. stricta* infestations have the capability of creating dense, impenetrable clumps, which smother indigenous vegetation and restrict the movement of mammals (Lotter & Hoffmann 1998). Due to the thorny nature of *O. stricta* coupled with the formation of dense impenetrable clumps, certain sampling techniques had to be excluded i.e. sweep netting and tree beating. Nevertheless, I expected that the spiders captured would be representative of the total spider community in the *O. stricta* invaded site. Moreover, I expected that sampling effort would be adequate to obtain a representative spider sample.

Thesis outline

The study is divided into four main sections: (1) a general introduction, (2) a critical evaluation of three sampling techniques used to sample spiders in a savanna invaded by *O. stricta*, (3) an evaluation of the impacts of *O. stricta* on beetle and spider assemblages and (4) a general discussion.

Chapter 1 is a general introduction including a review of the study species, an outline of the study area, objectives and aims, expected outcomes and a thesis outline.

Chapter 2 is a methodology paper, which critically evaluates the three sampling techniques (pitfall trapping, active searching and leaf litter sifting) used for collecting spiders in a savanna invaded by *O. stricta*. Due to the transformed nature of the site, certain traditional methods used for collecting spiders in a savanna (such as sweep netting and tree beating) could not be used. Recommendations for standardised sampling techniques are proposed and the minimum number of sampling events to reach inventory completion was calculated. Furthermore, a detailed appendix was produced which provides KNP management with a species checklist as well as contributing to the wider survey of arachnids in South Africa.

Chapter 3 focuses on assessing the impact of *O. stricta* infestation on beetle and spider assemblages and whether these assemblages differ between invaded treatments by identifying beetle and spider species characteristic of each *O. stricta* infestation level.

Chapter 4 is a general discussion of the results from Chapters 2 and 3, with application to management of *O. stricta* in KNP.

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CHAPTER 2

METHODOLOGY: A CRITICAL ASSESSMENT OF THE METHODS USED TO CAPTURE SPIDERS AND ASSESS THEIR ASSEMBLAGES IN AN ALIEN INVADED SAVANNA

INTRODUCTION

The threats to biodiversity are many and well documented (Ehrlich & Pringle 2008). They include habitat conversion, environmental toxification, climate change, direct exploitation of wildlife and biological invasions (Ehrlich & Pringle 2008). In reaction to these threats, there is an increasing drive to document and describe invertebrate diversity (Raven & Wilson 1992; Stork & Samways 1995; Samways 2007). Several sampling and estimation procedures have already been proposed for various invertebrate taxa including millipedes (Druce *et al.* 2004), spiders (Colwell & Coddington 1994), ground beetles (Niemelä *et al.* 2000) and ants (Agosti & Alonso 2000). Spider species richness data are increasingly incorporated into conservation and management decisions, as they are an ideal group to monitor the impacts of biological invasions on biodiversity (Kremen *et al.* 1993). Spiders are a highly diverse and abundant invertebrate group and their importance as indicators of habitat quality and change has been examined to some extent (e.g. New 1999; Pétillon *et al.* 2005; Pearce & Venier 2006; Scott *et al.* 2006). As a result, many studies have focused on developing sampling protocols that capture the greatest number of species (Coddington *et al.* 1996; Churchill & Arthur 1999; Sørensen *et al.* 2002; Jiménez-Valverde & Lobo 2005). Due to the large ecological diversity shown by spiders, a variety of sampling methods need to be used over time to ensure that species richness estimates are as accurate as possible (Jiménez-Valverde & Lobo 2006). Thus, in order to capture reliable and complete inventories, the design of the sampling protocol should combine various sampling methods, selecting the methods promising maximum information and complementarity for each environment and taxonomic group (Coddington *et al.* 1996; Green 1999; Sørensen *et al.* 2002).

For spiders, commonly used sampling methods include pitfall trapping, active searching, leaf litter sifting, sweep netting, tree beating and suction sampling. Pitfall trapping is one of the most widely employed methods as it is considered to be repeatable and often captures species active outside diurnal searching periods (New 1999; Slotow & Hamer 2000). However, one of the major drawbacks associated with pitfall trapping is the collection of non-target taxa and further concerns have been raised over the impact on long-lived or rare species (New 1999). Active searching methods allow for the capture of less mobile species, but are often considered less repeatable than pitfall trapping methods and comparisons with different habitats, incorporating different vegetal structure, can often be problematic (Churchill & Arthur 1999).

In the Kruger National Park (KNP), one of South Africa's largest, most well known protected areas, biological invasions are considered the greatest threat to biodiversity (Foxcroft & Freitag-Ronaldson 2004). *Opuntia stricta* (Haworth) Haworth (Cactaceae) was first observed in 1953 in the KNP and has subsequently invaded 35 000 ha of savanna habitat forming dense impenetrable thickets, which smother indigenous vegetation and restrict the movement and forage of animals (Lotter & Hoffmann 1998). It has been classed as a transformer species, which is an invasive species that changes the character, condition, form or nature of ecosystems over a substantial area (Richardson *et al.* 2000).

Assessing the impacts of biological invasions on biodiversity is of vital importance and is seen as a major priority by many conservation biologists and conservation managers (Byers *et al.* 2001). The impacts of *O. stricta* on arthropod assemblages in the KNP are not known and further still, it is not known how sampling methods commonly used in pristine ecosystems will perform in transformed habitats such as those affected by biological invasions. Knowledge regarding this topic is lacking, and to my knowledge, no other studies have been published. In the savanna biome Whitmore *et al.* (2002), found that more than one trapping method was required to sample the spider community in a savanna environment adequately. Whitmore *et al*. (2002) further suggests that surveys including sweeping, beating and active searching would be ideal for a representative sample. In this study, commonly used sampling techniques, such as sweep netting and tree beating, could not be utilised because of the thorns present on the *O.*

stricta plants. Furthermore, the dense nature of the *O. stricta* patches precluded the use of the tree beating technique. With this in mind, this methodology chapter aims to (1) assess the degree to which different methods often used to capture spider species complement each other in a highly transformed savanna habitat in the KNP and (2) evaluate these methods in terms of effort required to obtain representative species samples. The questions posed in this chapter are of utmost importance, as the findings are directly relevant to the methods used in Chapter 3 of this thesis.

MATERIAL AND METHODS

Study area

Spiders were collected in the Skukuza region of the KNP, South Africa (25º 00´S 31º 7´E) as this region is the most affected by *O. stricta* infestation (Foxcroft *et al.* 2007). The KNP is situated on the eastern side of the Limpopo and Mpumalanga provinces of South Africa and is bordered on its entire eastern side by Mozambique. The park falls within the savanna biome (Scholes 1997) and covers a surface area of 1 948 528 ha. The climate is subtropical and rainfall varies from 400 mm in the north to 700 mm in the south. The study site was situated in the Sabie/Crocodile thorn thicket habitat block (Gertenbach 1983) within the southern region of the KNP. This habitat is characterized by native woody species such as *Dichrostachys cinerea* Wight & Arn. (Mimosaceae), *Spirostachys africana* Sonder (Euphobiaceae) and *Grewia bicolor* Juss. (Malvaceae). *Panicum maximum* Jacq. (Poaceae), *Pogonarthria squarrosa* (Roem. & Schult.) Pilg. (Poaceae) and *Aristida congesta* Roem. & Schult. (Poaceae) are grasses that dominate the understory vegetation.

Experimental design

In order to compare the effectiveness of the different trapping methods for collecting spiders in areas invaded by *O. stricta*, four different treatments, containing five replicates each, were selected to represent a gradient in the level of *O. stricta* infestation. Treatments were selected according to the size (i.e. ground cover) of the *O. stricta* patch and each replicate was placed at least 50 m apart to prevent pseudo-replication of samples. Due to the overall size of the infestation, it was not possible to place the replicates further apart. First, high infestation treatments were defined as those with dense continuous cladodes covering a ground surface area larger than 10 x 10 m. Second, intermediate infestation treatments were defined as those with dense continuous cladodes covering a ground surface area larger than 6 x 3 m, but smaller than 10 x 10 m. Third, surrounded infestation treatments were treatments surrounded by *O. stricta* infestations, but contained no *O. stricta.* These treatments were almost completely surrounded by *O. stricta* infestations and therefore varied in size. However, most of the surrounded treatments covered a ground surface area of larger than 10 x 10 m. The surrounded treatments were also at least 50 m away from other treatments (Table 1). This treatment was selected due to the patchy nature of *O. stricta* infestation. Finally, the control treatments were pristine sites containing no *O. stricta* and were at least 50 m away from other treatments and covered a ground surface area larger than 10 x 10 m (Table 1). Sampling was conducted bi-monthly for twelve months between 2005 and 2006 (i.e. six sampling events), commencing in July 2005 and ending May 2006.

Sampling methods

Sampling for spiders in the transformed savanna utilised the following techniques: pitfall trapping, leaf litter sifting and active searching.

Pitfall trapping: Pitfall traps consisted of two-litre plastic buckets with a diameter of 20 cm filled with approximately 500 ml of water. In total, 100 pitfall traps were used with five traps placed in each replicate. Each trap was placed 1.5 m away from the other within the centre of the replicate in a circular pattern. During each sampling event, traps were left open for 10 days and cleared every second day. The contents of each trap were sieved, washed with water and were stored in 70 % ethanol. Traps were covered with a steel mesh grid to prevent the removal of contents by wild animals. A 10 cm gap was left between the steel grid and the ground, so that the trapping of spiders was unhindered.

Leaf litter sifting: A 1-m^2 quadrat was randomly placed within each replicate and all leaf litter was sifted through a 5 x 5 mm mesh. Specimens were then collected using an aspirator and stored in 70 % ethanol. During each sampling event, two leaf litter samples were taken at each replicate.

Active searching: Two 1-m^2 (2 m^2) quadrats were randomly placed within each replicate. At each replicate, all habitats suitable for spiders (including the ground, plants, rocks and fallen logs) were searched for 15 minutes (between 08h00 and 16h00). To prevent any collecting bias, the author conducted all active searching. Specimens were removed either by hand or by tweezers and deposited in 70 % ethanol. During each sampling event, two active searches were conducted at each replicate.

I identified spiders (adults and juveniles where possible) to family level, and further identification to species level was conducted by Dr Ansie Dippenaar-Schoeman. Some species could not be identified owing to the unresolved taxonomy of some families in Africa, e.g. Theridiidae and Lycosidae. Voucher specimens are housed in the National Collection of Arachnida (NCA) at the ARC-Plant Protection Research Institute.

Data analysis

Sample-based rarefaction curves were compiled using the analytically calculated S_{obs} (Mao Tao) (number of species expected) for each collecting method to establish sampling representivity using EstimateS V7.5 (Colwell 2005). The incidence-based coverage estimator (ICE; Chazdon *et al.* 1998) and Michaelis-Menten Mean (MMMean) estimators (Toti *et al.* 2000) were used to evaluate sample size adequacy. The ICE and MMMean richness estimators were chosen as they have performed well in previous spider inventory studies (Chazdon *et al.* 1998; Toti *et al.* 2000). The richness estimates may be considered representative when the observed sample-based rarefaction curves and the estimators converge closely at the highest observed richness (Longino *et al.* 2002). To establish overall sampling representivity, the total number of spiders captured were pooled for each replicate over the six sampling events (n=6). ICE and MMMean richness estimators were further used to evaluate sample size adequacy of spiders collected within the four treatments for each of the three different collecting methods (Chazdon *et al.* 1998; Toti *et al.* 2000). To estimate sampling representivity across the four treatments, the total number of spiders captured were pooled for each of the treatment replicates (n=5). Inventory completion was determined by calculating the observed species density as a percentage of the estimated species density using the MMMean richness estimator. To determine the minimum number of samples required to obtain a representative sample of the spiders present, the MMMean richness estimator and six sampling events were used in Equation 1 (Lovell *et al.* Unpublished report).

$$\text{Estimated no. of sampling events} = \frac{\text{estimated no. of individuals}}{(\Sigma \text{ individuals sampled/No. of sampling events sampled})}$$

Equation 1

Multivariate community analyses of the absolute spider abundance data were carried out using the PRIMER 5.2.0 software package (Clarke & Warwick 2001). A Bray-Curtis similarity measure was used to examine relationships between collecting methods for both overall abundance values (i.e. for the different treatments combined) and for those abundance values within each treatment. In order to account for differences in sampling effort (number of individuals collected) among the three collecting methods, species abundance data were used. Analysis of similarity (ANOSIM) was used to establish the significance of differences of spider assemblages between the different relationships examined. ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993); where the closer a significant global R-statistic is to one, the more distinct the differences.

Table 1. Coordinates for the four selected treatments (heavy infestation, medium infestation, pristine and surrounded) invaded by *Opuntia stricta* in the Kruger National Park

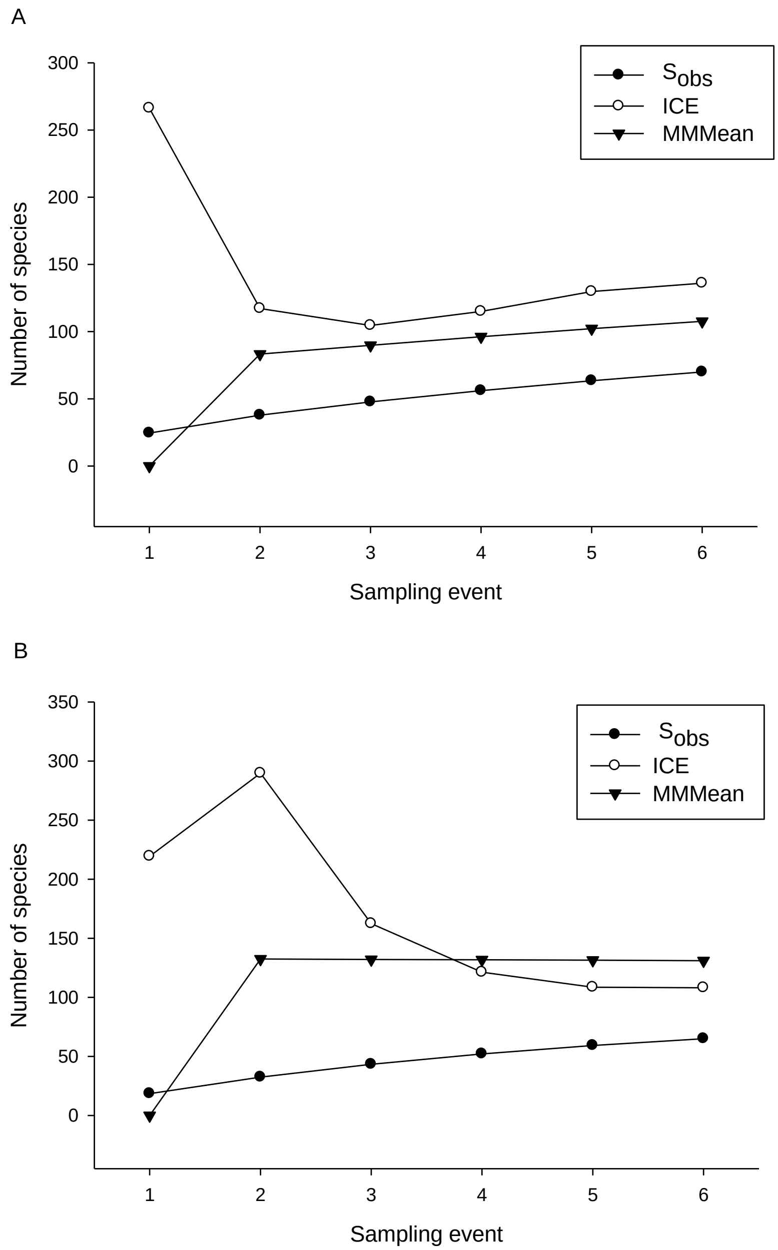
Treatment	**Coordinates**
	25º 0’ 39” S 31º 58’ 31” E
	25º 0’ 34” S 31º 58’ 32” E
Heavy Infestation	25º 0’ 34” S 31º 58’ 30” E
	25º 0’ 28” S 31º 58’ 30” E
	25º 0’ 31” S 31º 58’ 28” E
	25º 0’ 40” S 31º 58’ 31”E
	25º 0’ 36” S 31º 58’ 36” E
Medium Infestation	25º 0’ 40” S 31º 58’ 39” E
	25º 0’ 34” S 31º 58’ 36” E
	25º 0’ 31” S 31º 58’ 38” E
	25º 0’ 27” S 31º 58’ 38” E
	25º 0’ 27” S 31º 35’ 3” E
Pristine	25º 0’ 22” S 31º 58’ 28” E
	25º 0’ 23” S 31º 58’ 33” E
	25º 0’ 14” S 31º 35’ 0” E
	25º 0’ 28” S 31º 58’ 38” E
	25º 0’ 25” S 31º 58’ 37” E
Surrounded	25º 0’ 15” S 31º 35’ 5” E
	25º 0’ 26” S 31º 58’ 32” E
	25º 0’ 30” S 31º 58’ 33” E

RESULTS

One hundred and thirty one spider species, representing 1 050 individuals (adults and juveniles) in 96 genera and 28 families, were collected from the four treatments representing the gradient of *O. stricta* infestation in the KNP. Of these species, 54 species (41 %) are new records for the KNP (Appendix 1).

Comparison of trapping methods

Only 22 (17 %) species were collected by all three of the sampling methods used (Appendix 1). Of all the species collected, 21 %, 21 % and 15 % were unique to active searching, pitfall trapping and leaf litter sifting, respectively (Appendix 1). For each sampling method, the rarefaction curves and estimators did not converge closely with the highest observed overall richness indicating inadequate sampling effort (Fig. 1). The observed number of species (S_{obs}) fell well short of the estimated number of species calculated by the ICE and MMMean richness estimators (Table 2).


A
Sobs
ICE
MMMean
Number of species
300
250
200
150
100
50
0
1
2
3
4
5
6
Sampling event
B
Sobs
ICE
MMMean
Number of species
350
300
250
200
150
100
50
0
1
2
3
4
5
6
Sampling event

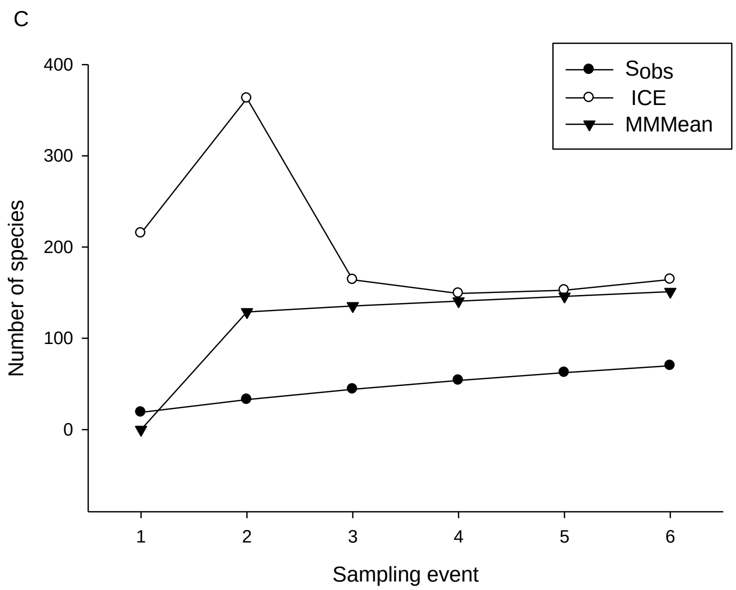


Fig. 1. Species rarefaction curves indicating observed number of species (S_{obs}), incidence-based coverage estimator (ICE) and Michaelis-Menten Mean (MMMean) richness estimators, for three different collecting methods in the Kruger National Park. A = pitfall trapping, B = leaf litter sifting and C = active searching (n=6 for each collecting method).

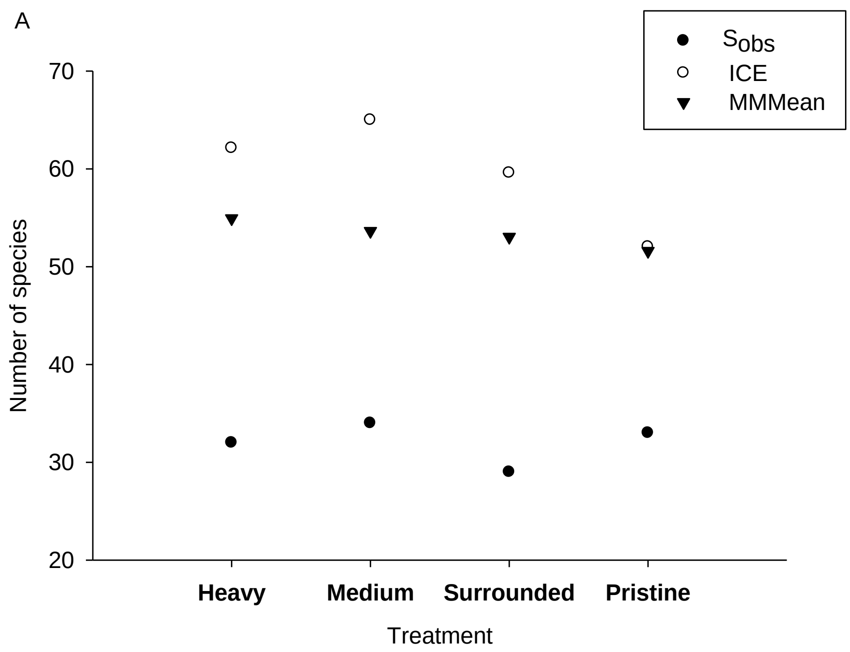
Table 2. Comparison between the observed (S_{obs}) and estimated number of species calculated using the incidence-based coverage estimator (ICE) and Michaelis-Menten Mean (MMMean) richness estimators. Inventory completion and minimum number of sampling events to reach inventory completion were calculated with MMMean richness estimator and six sampling events.

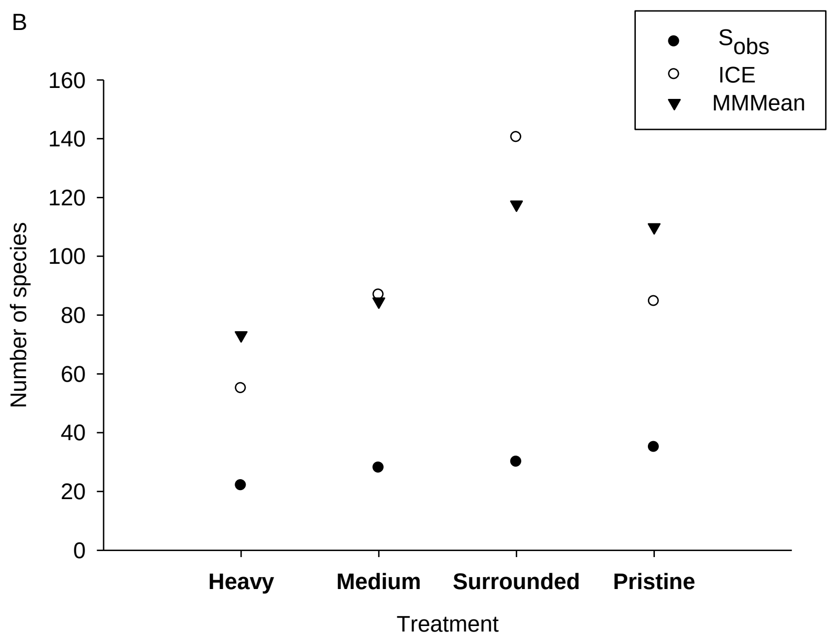
	Observed number of species	**Estimated number of species**		**Inventory completion**	**Minimum sampling events**
		ICE	MMMean		
Pitfall trapping	70	136	107	65.42 %	9
Leaf litter sifting	65	108	131	49.62 %	12
Active searching	70	164	151	46.36 %	13

Pitfall trapping was closest to producing a complete inventory (65.42 %), while both leaf litter sifting (49.62 %) and active searching (46.36 %) showed low values for inventory completeness (Table 2). To produce a complete inventory, all three collecting methods require more sampling events to create an adequate inventory (Table 2).

Although all treatments were, in general, under-sampled by the different collecting methods, certain treatments were better sampled than others for a given collecting method (Fig. 2). Treatments in which the observed richness (S_{obs}) is close to the estimated richness (ICE or MMMean) can be considered to have been better sampled than those in which observed richness is further from estimated richness (Fig. 2). For pitfall trapping, pristine sites were sampled best (Fig. 2A) while for leaf litter sifting, heavily invaded sites were sampled best (Fig. 2B) and for the active searching method, the surrounded sites were sampled best (Fig. 2C).

No single species was abundant in all three trapping methods (Fig. 3). Rather, each method was dominated by a different species. Lycosidae sp. 1 was the most abundant species captured in pitfalls, followed closely by *Hogna transvaalica* (Simon 1898) (Fig. 3A). In the case of leaf litter sifting and active searching, *Asemesthes* sp. 1 and *Hippasa australis* Lawrence 1927, respectively, were the most abundant species, although not more abundant than those species with a relative abundance of < 5 % that were grouped (Figs. 3B & C).


A
Sobs
ICE
MMMean
70
60
50
40
30
20
Number of species
Heavy
Medium
Surrounded
Pristine
Treatment


B
Sobs
ICE
MMMean
160
140
120
100
80
60
40
20
0
Number of species
Heavy
Medium
Surrounded
Pristine
Treatment

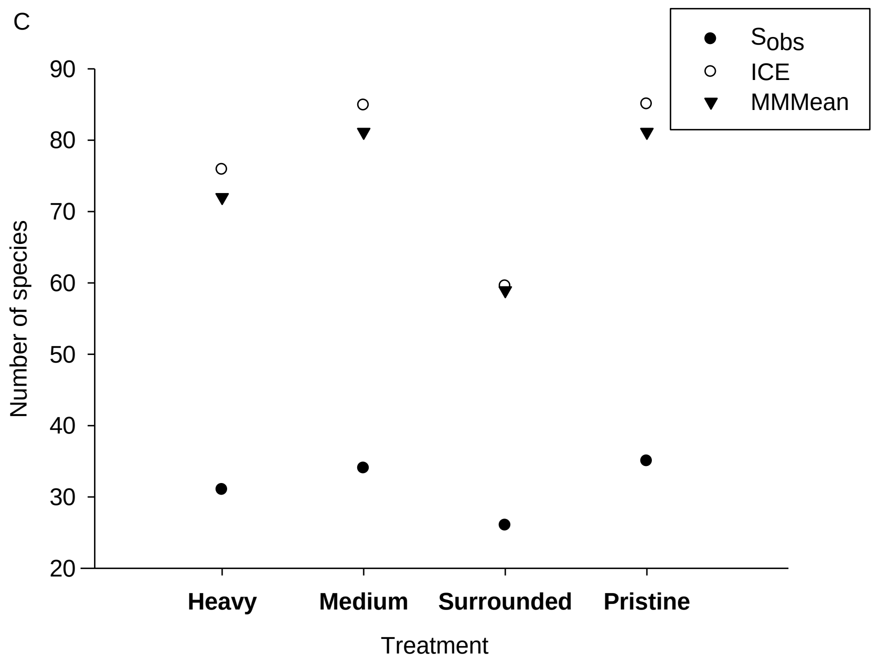
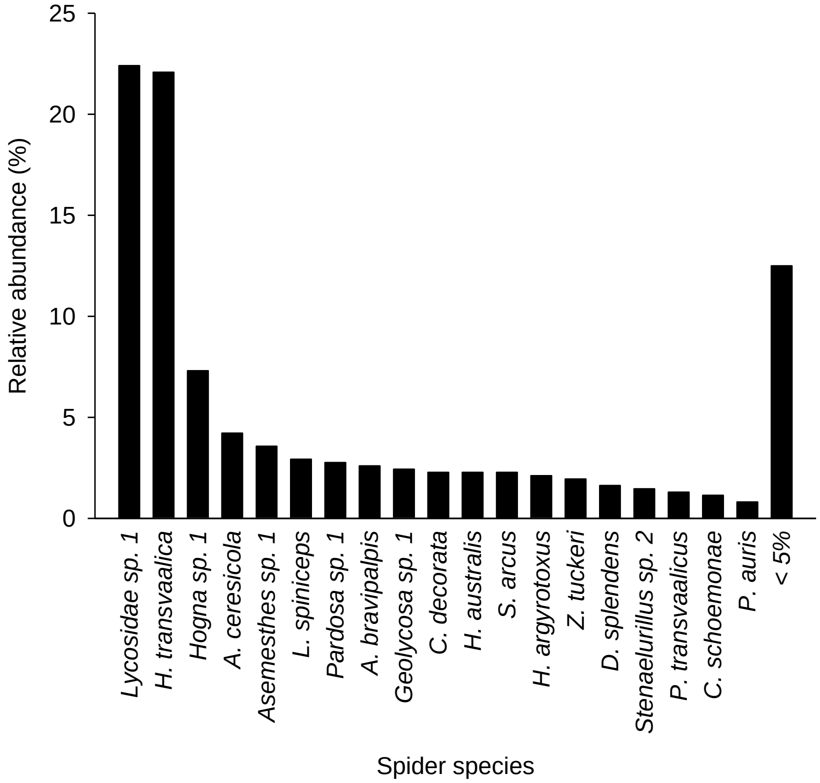


Fig. 2. Species richness estimation values for observed number of species (S_{obs}), incidence-based coverage estimator (ICE) and Michaelis-Menten Mean (MMMean) richness estimators for three different collecting methods in four different *O. stricta* infested treatments in the Kruger National Park. A = pitfall trapping, B = leaf litter sifting C = active searching (n=5 for each treatment).

Comparison of spider assemblages

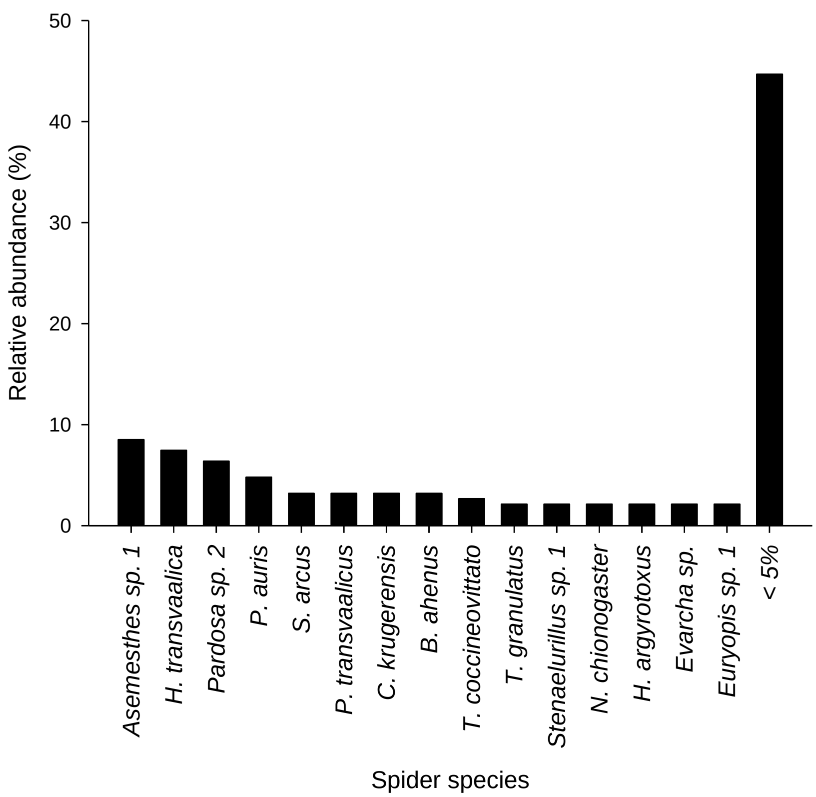
When compared among the three collecting methods using abundance data for the different treatments combined, the spider assemblages overlapped, but can be considered to be different or separable following Clarke & Warwick's (2001) classification of a significant Global R - value between 0.25 and 0.5 (Global $R = 0.36$, $p = 0.001$). Spider assemblages were barely separable when compared between leaf litter sifting and active searching (Global $R = 0.21$, $p = 0.008$) but there was greater separation between leaf litter sifting and pitfall trapping (Global $R = 0.41$ $p = 0.002$) and between active searching and pitfall trapping (Global $R = 0.45$ $p = 0.002$). Examining each treatment separately, spider assemblages, for both the pristine and surrounded sites, were very similar when compared between all possible pairs of sampling methods with a Global R varying between 0.14 and 0.33 ($p < 0.05$). In the medium and heavy infestation treatments, assemblage differences were more pronounced at least when compared between pitfall trapping and leaf litter sifting (Global $R = 0.59$, $p = 0.008$), and between pitfall trapping and active searching (Global $R = 0.56$, $p = 0.016$), respectively.

A



Relative abundance (%)
25
20
15
10
5
0
Lycosidae sp. 1
H. transvaalica
Hogna sp. 1
A. ceresicola
Asemesthes sp. 1
L. spiniceps
Pardosa sp. 1
A. bravipalpis
Geolycosa sp. 1
C. decorata
H. australis
S. arcus
H. argyrotoxus
Z. tuckeri
D. splendens
Stenaelurillus sp. 2
P. transvaalicus
C. schoemonae
P. auris
< 5%
Spider species

B



Relative abundance (%)
50
40
30
20
10
0
Asemesthes sp. 1
H. transvaalica
Pardosa sp. 2
P. auris
S. arcus
P. transvaalicus
C. krugerensis
B. ahenus
T. coccineovittato
T. granulatus
Stenaelurillus sp. 1
N. chionogaster
H. argyrotoxus
Evarcha sp.
Euryopis sp. 1
< 5%
Spider species

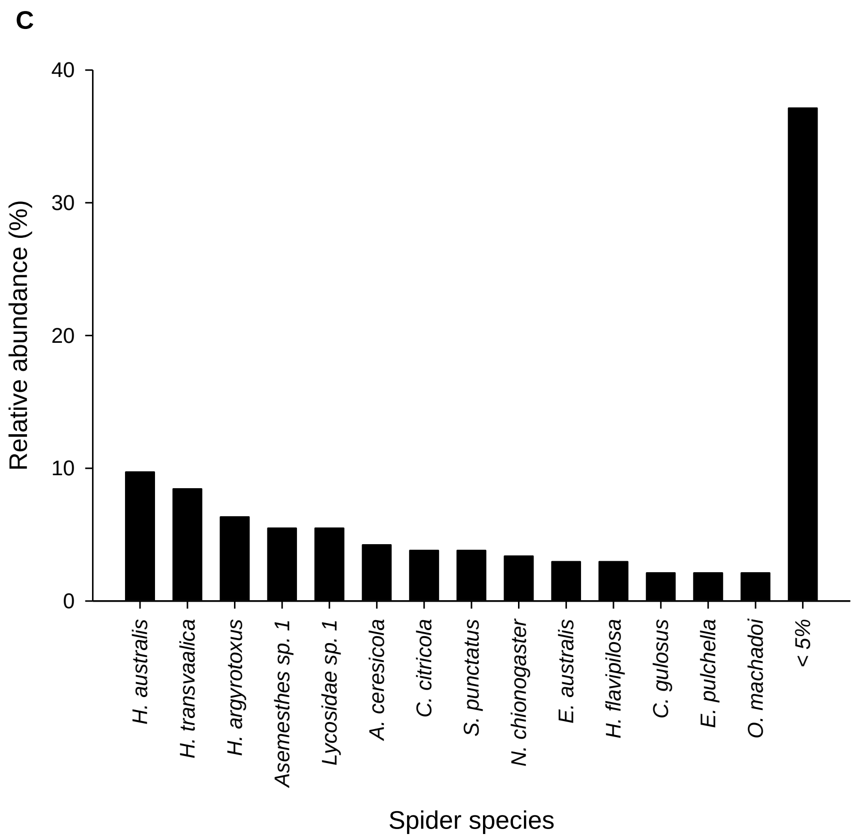


Fig. 3. Spider species rank abundance for three different trapping methods in the Kruger National Park. Species with a relative distribution of less than five percent were added together. A = pitfall trapping, B = leaf litter sifting and C = active searching.

DISCUSSION

Although all three methods under-sampled to some extent, the 28 spider families collected in the study represent 47 % of the recorded spider families found in South Africa (Dippenaar-Schoeman & Jocqué 1997), and the number of species collected compares favourably with other studies undertaken in the savanna biome (Whitmore *et al.* 2002; Dippenaar-Schoeman & Leroy 2003). Moreover, the current study adds 54 new spider records to KNP's inventory and includes a new family record namely Agelenidae. No species of significant conservation importance were collected. Under-sampling of the spider fauna is a problem that is common to most spider related studies (Coddington *et al.* 1996) and even after conducting intensive sampling efforts, studies have often been unable to sample the entire range of spider species associated with a given area (Toti *et al.* 2000; Sørensen *et al.* 2002). The large number of singletons sampled (36 %) may be a result of the under-sampling of the three methods and inventory completion may be a matter of more sampling (Colwell & Coddington 1994; Sørensen *et al.* 2002). However, some or many of these singletons may be temporal singletons or artefacts of temporally patchy sampling and therefore more sampling may be required (Toti *et al.* 2000).

All three of the collecting methods used in this study show a level of complementarity since the assemblages were distinguishable and in some cases clearly different. With only 17 % of the species shared between methods, this study suggests that the methods used performed relatively well within a savanna invaded by *O. stricta* at least from a complementary point of view.

Pitfall traps captured more species in the pristine sites when compared with heavy and medium infested sites. Impedance, due to the ground level complexity in the heavy and medium infested sites, may account for the lower trap success in these sites when compared with pristine sites, which are less structurally complex. Habitat structure has been shown to affect pitfall trap success by affecting the movement behaviour of animals, either through microclimatic conditions or by a more direct response by individuals to the physical properties of the habitat (Melbourne 1999). This suggests that in savannas invaded by *O. stricta*; heavily invaded sites may require a greater pitfall sampling effort. In contrast, the leaf litter sifting method performed well in heavily invaded sites, which may be due to the large amount of leaf litter and other decaying plant material found in these treatments. Active searching performed well in the surrounded sites most likely due to the sparse cover of vegetation in this treatment.

In order to improve the inventory completeness of spider species in the *O. stricta* invaded sites of KNP, as calculated by the MMMean richness estimator in this study, more replicates, both spatially and temporally, are required. A study conducted in the Western Cape, South Africa by Boonzaaier *et al.* (2007) found that increases in sampling effort in terms of increasing the sampling duration and sampling intensity (more spatial replicates) resulted in a similar increase in ant species richness captured. However, they also showed that there was a greater rate of species turnover associated with different spatial replicates compared to temporal replicates (see also Delabie *et al.* 2000).

Considering the results from Boonzaaier's (2007) study, together with those from this study and the patchy nature of the *O. stricta* invasion, I suggest the following recommendations to sample spiders within a savanna habitat characterized by *O. stricta* invasion. First, if financial costs and time does not allow for the use of all three the methods used here, priority should be given to leaf-litter sifting and active searching methods as they performed best in a *O. stricta* invaded environment compared to pitfall trapping. Active searching also scored the highest estimated number of species compared to leaf litter sifting and pitfall trapping, and together with pitfall trapping scored the highest observed number of species (Table 1). Considering the sampling efforts of this study, leaf litter sifting and active searching methods require at least six additional sampling events each to achieve a value more representative of a complete inventory (see Table 1). However, considering the relative small size of the *O. stricta* patches and the small total area invaded, at least in the KNP, such an increase in sampling intensity for spatial replicates will be more difficult to achieve compared to temporal replicates. Although the former approach compared to the latter has been recommended by Boonzaaier's (2007) ant study, it is well known that spiders show high levels of temporal turnover in species composition, even within a short time period (Toti *et al.* 2000) and such a high turnover is probably not as significant within ants.

Second, I suggest increasing the amount of time that the pitfall traps are open from 10 days (used for this study) to at least 15 days based on the percentage inventory completion result of 65% for this study (Table 2). This would be a cost effective way of increasing the inventory completeness and a more practical approach seeing that a further increase in spatial replicates compared to the effort already used in this study will be difficult to achieve given the current spatial scale and patchy distribution of the *O. stricta* invasion in KNP. However, by increasing the number of temporal replicates the populations of long-lived families, such as the Theraphosidae (baboon spiders) and Idiopidae (trap door spiders) may be negatively impacted by continual removal.

In conclusion, this study shows that sampling methods often used to capture spiders in savanna environments can also be used in a highly transformed savanna habitat invaded by *O. stricta* to compile a species inventory. Although all three methods complemented each other significantly, and should be used in combination, the spider biodiversity associated with the transformed areas was better captured via the leaf litter sifting and active searching methods compared to the pitfall trapping method. Furthermore, leaf litter sifting and active searching allows more opportunity to maximize sampling efforts in a qualitative way by increasing both sampling intensity and sample duration compared to pitfall trapping given the small and highly patchy nature of the *O. stricta* invaded sites in KNP. Due to the large number of singletons collected and the relative incompleteness of the spider survey, studies in the future should perhaps focus on other taxa (such as ants, millipedes), which may be more representative and easier to capture.

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Appendix 1. The total number of spiders, listed per family, collected in the Kruger National Park using pitfall trapping (PT), leaf litter sifting (LLS) and active searching (AS). Species names marked with * represent new records for the region. Spider genera were assigned to three functional groups as proposed by Dippenaar-Schoeman & Leroy (2003); including ground-wanderers (GW), plant-wanderers (PW) and web-builders (WB).

Species	Functional group	PT	LLS	AS
Agelenidae				
Agelena sp. 1*	GW			2
Benoitia ocellata (Pocock, 1900)*	GW	1		
Araneidae				
Argiope australis (Walckenaer, 1805)	WB			1
Argiope lobata (Pallas, 1772)*	WB			1
Caerostris sexcuspidata (Fabricius, 1793)	WB			3
Chorizopes sp. 1*	WB			2
Cyphalonotus larvatus (Simon, 1881)	WB			1
Cyrtophora citricola (Forskål, 1775)	WB			9
Hypsosinga lithyphantoides Caporiacco, 1947*	WB		1	2
Isoxya stuhlmanni (Bösenberg & Lentz, 1895)	WB			3
Neoscona blondeli (Simon, 1885)	WB		1	3
Prasonica sp. 1	WB			1
Pararaneus sp. 1*	WB			1
Singa albodorsata Kauri, 1950	WB		1	
Caponiidae				
Caponia natalensis (O.P.-Cambridge, 1874)	GW	1	3	

Corinnidae				
Castianeira sp. 1	GW			1
Copa flavoplumosa Simon, 1885*	GW	1		
Corinnomma semiglabrum (Simon, 1896)*	GW			1
Messapus sp. 1*	GW	2		
Merenius alberti Lessert, 1921	GW	2	1	2
Ctenidae				
Anahita sp. 1	GW			1
Ctenus gulosus Des Arts, 1912	GW	1	1	5
Cyrtaucheniidae				
Ancylotrypa barbertoni (Hewitt, 1913)	GW	1		
Ancylotrypa brevipalpis (Hewitt, 1916)*	GW	16		
Ancylotrypa sp. 1*	GW	4		
Ancylotrypa sp. 2*	GW	1		
Ancylotrypa sp. 3*	GW	1		
Dictynidae				
Mashimo leleupi Lehtinen, 1967	WB		1	
Eresidae				
Adonea sp. 1*	WB	1		
Gnaphosidae				
Aphantaulax inornata Tucker, 1923	GW		3	
Asemesthes ceresicola Tucker, 1923*	GW	26	1	10
Asemesthes numisma Tucker, 1923	GW	1		
Asemesthes purcelli Tucker, 1923	GW	1		
Asemesthes sp. 1*	GW	22	16	13

Camillina corrugata (Purcell, 1907)	GW	2	3	2
Drassodes masculus Tucker, 1923*	GW	5		1
Drassodes splendens Tucker, 1923*	GW	10		
Drassodes sp. 1	GW	1		
Pterotricha auris (Tucker, 1923)	GW	5	9	2
Setaphis arcus Tucker, 1923	GW	14	6	
Setaphis browni (Tucker, 1923)	GW		1	
Xerophaeus sp. 1	GW	2		2
Zelotes oneili (Purcell, 1907)*	GW	1		
Zelotes tuckeri Roewer 1951*	GW	12	3	
Zelotes ungulus Tucker, 1923*	GW	1		
Zelotes sp. 1	GW		1	
Idiopidae				
Segregara mossambicus (Hewitt, 1919)*	GW	1		
Lycosidae				
Arctosa sp. 1	GW	1		
Geolycosa sp. 1	GW	15	2	
Hippasa australis Lawrence, 1927	GW	14	1	25
Hogna transvaalica (Simon, 1898)	GW	135	14	20
Hogna sp. 1	GW	45	2	2
Lycosa sp. 1	GW	1		
Lycosidae sp. 1	GW	138		13
Ocyale sp. 1	GW	1		
Pardosa sp. 1*	GW	17		1
Pardosa sp. 2*	GW		12	3
Trabea sp. 1	GW	1		
Miturgidae				
Cheiracanthium furculatum Karsch, 1879	PW			3

Cheiramiona krugerensis Lotz, 2002	PW		6	
Oxyopidae				
Oxyopes falconeri Lessert, 1915*	PW	2	1	1
Oxyopes hoggi Lessert, 1915*	PW	1	1	1
Oxyopes jacksoni Lessert, 1915	PW			1
Oxyopes longispinosus Lawrence, 1938	PW			3
Oxyopes pallidecoloratus Strand, 1906	PW	1		1
Oxyopes sp. 1	PW	2	3	
Oxyopes sp. 2	PW			1
Peucetia sp. 1	PW		2	
Palpimanidae				
Diaphorocellus biplagiatus Simon, 1893	GW	2	1	
Palpimanus transvaalicus Simon, 1893	GW	8	6	1
Philodromidae				
Hirriusa variegata (Simon, 1895)	PW	2	1	2
Philodromus sp. 1	PW			3
Suemus punctatus Lawrence, 1938	PW		1	9
Pholcidae				
Smeringopus natalensis Lawrence, 1947	WB		1	
Spermophora sp. 1*	WB		1	
Pisauridae				
Afropisaura rothiformis (Strand, 1908)	WB	1	2	1
Euprosthenops australis Simon, 1898	WB			7
Euprosthenopsis pulchella (Pocock, 1902)*	WB			5
Maypacius bilineatus Pavesi, 1895*	WB			2

Prodidomidae				
Prodidiomus sp. 1*	GW	1		
Salticidae				
Aelurillus sp. 1	PW	1		
Baryphas ahenus Simon, 1902	PW	1	6	
Evarcha sp. 1	PW	1	1	4
Hyllus argyrotoxus Simon, 1902*	PW	13	4	15
Hyllus treleaveni Peckham & Peckham, 1902*	PW	1	1	4
Langelurillus sp. 1*	PW	2	3	
Langona sp. 1*	PW	1		
Mexcala sp. 1*	PW		1	1
Natta chionogastra (Simon, 1901)*	PW		4	8
Stenaelurillus sp. 1*	PW	2	5	3
Stenaelurillus sp. 2*	PW	9		1
Stenaelurillus sp. 3*	PW	2		2
Stenaelurillus sp. 4*	PW	2	2	3
Thyene coccineovittata (Simon, 1885)	PW		5	1
Thyenula sp. 1*	PW	2		
Scytodidae				
Scytodes constellata Lawrence, 1938*	GW	2		
Scytodes trifoliata Lawrence, 1938*	GW		1	
Sicariidae				
Loxosceles spiniceps Lawrence, 1952	GW	18		1
Sparassidae				
Olios correvoni Lessert, 1921	PW	1	3	
Olios machadoi Lawrence, 1952*	PW	3	3	5
Olios tuckeri Lawrence, 1927*	PW		1	1

Panaretella sp. 1	PW	1	1	1
Panaretella zuluana Lawrence, 1937*	PW	2		
Tetragnathidae				
Leucauge festiva (Blackwall, 1866)	WB			1
Theraphosidae				
Augacephalus breyeri (Hewitt, 1919)	GW	2		1
Ceratogyrus bechuanicus Purcell, 1902	GW			1
Ceratogyrus dolichocephalus Hewitt 1919	GW			1
Harpactirella flavipilosa Lawrence, 1936*	GW	3	2	7
Idiothele nigrofulva (Pocock, 1898)	GW	2		1
Pterinochilus lugardi Pocock, 1900*	GW	1		1
Theridiidae				
Argyrodes convivans Lawrence, 1937	WB			1
Chorizopella tragardhi Lawrence, 1947*	WB		1	
Dipoena sp. 1*	WB		3	
Euryopis sp. 1	WB		4	3
Latrodectus geometricus C.L. Koch, 1841	WB			1
Thomisidae				
Diaea puncta Karsch, 1884*	PW			1
Heriaeus fimbriatus Lawrence, 1942*	PW		3	
Monaeses pustulosus Pavesi, 1895	PW		3	
Monaeses quadrituberculatus Lawrence, 1927	PW			2
Runcinia flavida (Simon, 1881)	PW		2	1
Simorcus cotti Lessert, 1936	PW		1	
Stiphropus sp. 1*	PW		1	
Thomisops pupa Karsch, 1879	PW		1	
Thomisus daradioides Simon, 1890	PW		1	

Thomisus granulatus Karsch, 1880	PW		4	1
Xysticus lucifugus Lawrence, 1937*	PW		1	
Uloboridae				
Miagrammopes longicaudus (O.P.-Cambridge, 1882)	WB			1
Zodariidae				
Capheris decorata Simon, 1904	GW	14		
Cydrela schoemanae Jocqué, 1991	GW	7	2	1
Cydrela sp. 1	GW		1	
Ranops caprivi Jocqué, 1991	GW	1	1	
Number of species		**71**	**65**	**75**
Number of unique species		**28**	**20**	**28**
Number of individuals		**619**	**182**	**249**

CHAPTER 3

ASSESSING LOCAL SCALE IMPACTS OF *OPUNTIA STRICTA* (CACTACEAE) INVASION ON BEETLE AND SPIDER ASSEMBLAGES IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

ABSTRACT

In the Kruger National Park (KNP), introduced prickly pear (*Opuntia stricta*) has invaded some 35 000 ha of conserved land and its impacts on biodiversity are a major cause for concern. To quantify these impacts, the effect of *O. stricta* infestation on beetle (Order Coleoptera) and spider (Order Araneae) species assemblages in the Skukuza region of the KNP was investigated using unbaited pitfall traps over a 12-month period. Four treatments of varying *O. stricta* infestation were identified: heavy infestation, medium infestation, surrounded sites and pristine sites (non-invaded). Species characteristic of each treatment (indicator species) were identified using the indicator method (IndVal). Species richness, species density and abundance of beetles and spiders were compared. A total of 72 beetle and 129 spider species were collected. No species fulfilled the criteria for the indicator species concept. Species richness and species density for beetles and spiders did not differ significantly across the four treatments. The study concludes that at the current infestation level, *O. stricta* does not have a significant effect on beetle or spider species richness or density. However, further examination of other arthropod groups is required to understand the effects of the *O. stricta* infestation and a continued biocontrol programme is essential to mitigate the effects of *O. stricta* on biodiversity.

INTRODUCTION

Invasive alien organisms and their overall negative effects on biodiversity and ecosystem services, and thus ultimately on human well-being, are a major global problem (Vitousek *et al.* 1997; Sala *et al.* 2000; Le Maitre *et al.* 2004; Clavero & Garciá-Berthou 2005; van Wilgen *et al.* 2008). For some countries, this issue is one of the most challenging environmental threats of the 21st century (see e.g. Stohlgren *et al.* 2006 for the USA). In New Zealand, for most threatened animal and plant species invasive species now pose the greatest remaining threat to their continued survival. Although the greatest threat here is arguably from introduced mammals, many invasive plants have the ability to alter native ecosystems over a long period of time (Clout & Lowe 2000). Similarly, Chile is plagued with a large number of invasive plants with a total number of 690 aliens species contained in 73 families and 37 genera that have become naturalized in continental Chile since the colonial period (Arroyo *et al.* 2000). In South Africa, natural ecosystems are threatened by invasive alien plants with almost 10 million ha (8.28 %) of the region invaded to some extent (Le Maitre *et al.* 2000). These threats include impacts on ecosystem functioning in the delivery of goods and services (Richardson & van Wilgen 2004), impacts on surface water resources (Le Maitre *et al.* 2000; 2002; Görgens & van Wilgen 2004), and increase in biomass leading to increased fuel loads (van Wilgen & Richardson 1985).

For certain species or biological groups, the patterns of invasions have been reasonably well documented at various spatial scales (Kennedy *et al.* 2002; Stohlgren *et al.* 2003; Fridley *et al.* 2007). However, there is less quantitative information on defining and measuring the ecological impacts of invasions and how these impacts vary for different species in different geographical areas (van Wilgen 2004). As for South Africa, the impacts of invasive species, especially harmful plants, on invertebrate biodiversity are poorly known (Samways & Moore 1991; Steenkamp & Chown 1996; French & Major 2001; Samways & Taylor 2004; Coetzee *et al.* 2007). Globally there is also little known about the impacts of invasive species on invertebrate diversity (Gratton & Denno 2005). With invertebrates contributing the bulk of global species diversity and regulating many processes fundamental to structure and function in most biomes throughout the world (Wilson 1987), quantifying these impacts is of vital importance.

Invertebrates are increasingly used as bioindicators in a variety of roles (Noss 1990; McGeoch 1998; Andersen & Majer 2004) and could serve as valuable tools in monitoring the effects of invasive plants. Bioindicators are classified into three categories: biodiversity, environmental and ecological indicators (see McGeoch 1998 for additional discussion). A biodiversity indicator provides information on the presence of a set of other species and provides a descriptive function (Pearce & Venier 2006). Environmental indicators indicate change in the state of the abiotic environment directly, while ecological indicators demonstrate the effects of environmental change on the biotic systems including species, communities and ecosystems (McGeoch 1998; Pearce & Venier 2006). Spiders (Araneae) constitute a highly diverse group and their position in the trophic level and mobility suggest that they are ideal candidates for use as bioindicators (Churchill 1997). Several studies have already advocated the use of spiders as indicators of habitat quality and change in a variety of habitats (Pétillon *et al.* 2005; Scott *et al.* 2006). Dung beetles (Scarabaeidae) and ground beetles (Carabidae) have also been shown to be good indicators of habitat quality and change, due to their sensitivity to habitat modification and have consequently been used in several studies (van Rensburg *et al.* 1999; McGeoch *et al.* 2002; Rainio & Niemelä 2003; Coetzee *et al.* 2007). Pearce & Venier (2006) have advocated using both spiders and ground beetles to evaluate the impact of habitat fragmentation and the creation of forest edges in natural boreal forests in Canada in order to assess sustainability in silvicultural practices.

Within the Kruger National Park (KNP), which is considered the flagship reserve within South Africa's protected area network (Carruthers 1995), alien invasive plants have been identified as the greatest threat to biodiversity ahead of traditional threats such as fragmentation and poaching (Foxcroft & Freitag-Ronaldson 2004). *Opuntia stricta* (Haworth) Haworth (Cactaceae) is the most widespread of these invasive plants and since it was first recorded in 1953 it is estimated that the plant has invaded 35 000 ha (2 %) of KNP's surface area (Foxcroft *et al.* 2007). Initial attempts to control the plant began in 1985 and depended largely on herbicidal applications and mechanical removal but more recently, the emphasis has shifted to biological control (Lotter & Hoffmann 1998). The biological control programme is reliant on two agents; the cactus moth, *Cactoblastis cactorum* (Lepidoptera: Pyralidae) (Hoffmann *et al.* 1998a) and a cochineal insect, *Dactylopius opuntiae* (Homoptera: Dactylopiidae). Both have played a major role in managing the weed (Foxcroft & Hoffmann 2000).

The management of alien invasive organisms in KNP is based largely on the concept of Thresholds of Potential Concern (TPCs). These thresholds represent the upper and lower limits of acceptable change in ecosystem structure, function and composition over time and at a specified spatial scale (Foxcroft & Richardson 2003). The threshold is breached when one or more of these limits are exceeded. Once exceeded, appropriate management interventions are then implemented. The alien invasive species TPCs are divided into three distinct management responses or levels relating to the invasion process or pathway (Foxcroft & Downey 2008). The TPCs are:

1. Level 1 TPCs target new or potential invasions or incursions within the KNP
2. Level 2 TPCs target increases in the distribution of alien species already in the KNP
3. Level 3 TPCs target increases in the density of an alien species in the KNP.

The level 3 TPC is stated as a hypothesis due to the lack of data on acceptable thresholds relating to density related impacts and the availability of efficient cost-effective monitoring protocols to detect such thresholds (Foxcroft & Downey 2008). However, an increase in density could potentially be used as a surrogate measure for an increase in biodiversity impact (Foxcroft & Downey 2008).

Little is known about the effects of *O. stricta* invasion on arthropod assemblages and no other studies have investigated this issue within KNP. In keeping with the KNP's alien impact objective, which is to minimize the influence of non-indigenous organisms on native biodiversity, the primary aim of the study was to assess the impact of *O. stricta* infestation on beetle and spider assemblages by considering different levels of infestation. The secondary aim was to identify beetle and spider species that are characteristic of each *O. stricta* infestation level and that can be used as potential ecological indicator species to assist with programmes monitoring the effects of invasive plants.

MATERIAL AND METHODS

Study area

Fieldwork was conducted in the Skukuza region of the KNP, South Africa (25º 00´S 31º58´E) as this region has been most heavily invaded by *O. stricta* (Foxcroft *et al.* 2007). The KNP is situated on the eastern side of the Limpopo and Mpumalanga provinces of South Africa and is bordered by Mozambique to the east. The park falls within the savanna biome (Scholes 1997) and covers a surface area of 1 948 528 ha. The climate is subtropical and rainfall varies from 400 mm in the north to 700 mm in the south. The study site was situated in the Sabie-Crocodile thorn thicket habitat type (Gertenbach 1983) in the southern region of the KNP. This habitat is characterized by native woody species such as *Dichrostachys cinerea* Wight & Arn. (Mimosaceae), *Spirostachys africana* Sonder (Euphobiaceae) and *Grewia bicolor* Juss. (Malvaceae). *Panicum maximum* Jacq. (Poaceae), *Pogonarthria squarrosa* (Roem. & Schult.) Pilg. (Poaceae) and *Aristida congesta* Roem. & Schult. (Poaceae) are grasses that dominate the understory vegetation.

Experimental design

In order to compare the effect of *O. stricta* infestations on beetle and spider assemblages, four different treatments, containing five replicates each, were selected to represent a gradient in the level of *O. stricta* infestation. Treatments were selected according to the size (i.e. ground cover) of the *O. stricta* patch and each replicate was placed at least 50 m apart to prevent pseudo-replication of samples. Due to the overall size of the infestation, it was not possible to place the replicates further apart. First, high infestation treatments were defined as those with dense continuous cladodes covering a ground surface area larger than 10 x 10 m. Second, intermediate infestation treatments were defined as those with dense continuous cladodes covering a ground surface area larger than 6 x 3 m, but smaller than 10 x 10 m. Third, surrounded infestation treatments were treatments surrounded by *O. stricta* infestations, but contained no *O. stricta*. These treatments were almost completely surrounded by *O. stricta* infestations and therefore varied in size. However, most of the surrounded treatments covered a ground surface area of larger than 10 x 10 m. The surrounded treatments were also at least 50 m away from other treatments. This treatment was selected due to the patchy nature of *O. stricta* infestation. Finally, the control treatments were pristine sites containing no *O. stricta* and were at least 50 m away from other treatments and covered a ground surface area larger than 10 x 10 m (Table 1). Sampling was conducted bi-monthly for twelve months between 2005 and 2006 (i.e. six sampling events), commencing in July 2005 and ending May 2006.

Ambient temperature measurements

Temperature dataloggers, type DS1921G (Dallas Semiconductor 2005), were used to record ambient temperature at one hour intervals over the full year of sampling. Two dataloggers were used for each treatment and were buried ± 2 cm below the soil surface. Mean monthly temperature was compared between the four treatments using ANOVA.

Vegetation sampling

Vegetation structure and species composition for each of the replicates was sampled during winter (August 2006) and summer (March 2007). At each replicate, a 10 x 10 m plot was measured, which surrounded the centre of the *O. stricta* patch. Eight, 1 m^2 quadrats were laid out on the inner edge of the 10 x 10 m plot and the following vegetation parameters were recorded: species composition and percentage cover. To quantify the extent of *O. stricta* infestation surrounding the treatments, four 10 m line transects were extended outwards from the corners of each 10 x 10 m plot at a 45º angle and four 10 m transects were extended from the centre of the boundary of the 10 x 10 m plot at a 90º angle. On each line transect, the frequency of *O. stricta* occupying it was recorded. The frequency of *O. stricta* occurrence was then calculated for 50 cm distance classes along the transects for each replicate and treatment.

Beetle and spider sampling

During each sampling event, beetles and spiders were collected using pitfall traps and spiders were sampled additionally using leaf litter sifting and active searching methods. Based on results from Chapter 2, I have suggested that in a savanna habitat characterized by *O. stricta* invasion three trapping methods (pitfall trapping, leaf litter sifting and active searching) should be utilized in order to adequately sample spider species density and abundance. Although tree beating and sweep netting are frequently used to collect spiders in savanna environments, it was not possible to use these methods due to the transformed nature of the vegetation structure in the *O. stricta* infested sites.

Pitfall trapping: Pitfall traps consisted of two-litre plastic buckets with a diameter of 20 cm filled with approximately 500 ml of water. In total, 100 pitfall traps were used with five traps placed in each replicate. Each trap was placed 1.5 m away from the next within the replicate in a circular pattern. During each sampling event, traps were left open for 10 days and cleared every second day. The contents of each trap were sieved, washed with water and were stored in 70 % ethanol. Traps were covered with a steel mesh grid to prevent the removal of contents by wild animals. A 10 cm gap was left between the steel grid and the ground, so that the trapping of spiders and beetles was unhindered.

Leaf litter sifting: A 1-m^2 quadrat was randomly placed within each replicate and all leaf litter was sifted through a 5 x 5 mm mesh. Specimens were then collected using an aspirator and stored in 70 % ethanol. During each sampling event, two leaf litter samples were taken at each replicate.

Active searching: Two 1-m^2 (i.e. total of 2 m^2) quadrats were randomly placed within each replicate. At each replicate, all habitats suitable for spiders (including the ground, plants, rocks and fallen logs) were searched for 15 minutes (between 08h00 and 16h00). To prevent any collecting bias, the author conducted all active searching. Specimens were removed either by hand or by tweezers and deposited in 70 % ethanol. During each sampling event, two active searches were conducted at each replicate.

Spiders were identified to family level, and then where possible, Prof A. Dippenaar-Schoeman (ARC-PPRI) identified the specimens to species level. Some species could not be identified owing to the unresolved taxonomy of some families in Africa, e.g. Theridiidae and Lycosidae. Spider voucher specimens are housed in the National Collection of Arachnida (NCA) at the ARC-Plant Protection Research Institute, South Africa. Beetles were identified to species level where possible with help from

James Harrison at the Transvaal Museum, South Africa. Beetle voucher specimens are housed at the Transvaal Museum.

Fig. 1. Patchy nature of *Opuntia stricta* infestation in the Skukuza region of the Kruger National Park.

Data analysis

Vegetation

In order to quantify the level of the infestation surrounding each plot, the amount of *O. stricta* observed on each line transect was averaged for each replicate. Cover estimates for the two sample periods were averaged (August 2006 and March 2007). Plant species assemblages (of both *O. stricta* and natural vegetation) of the four treatments were compared using an analysis of similarity (ANOSIM) implemented in the PRIMER 5.2.0 software package (Clarke & Warwick 2001) where the closer a significant Global R statistic is to one, the more distinct the differences. Common and rare species were weighted equally by double square-root transformation of the data before analysis. A Bray-Curtis similarity measure was used to calculate the similarity matrix.

Beetles and spiders

Sample-based rarefaction curves were compiled for the total number of beetles and spiders collected in the study to establish sampling representivity using the analytically calculated S_{obs} (Mao Tao) of EstimateS V7.5 (Colwell 2005). For both spiders and beetles, the total number of species captured were pooled for each replicate over the six sampling events i.e. five replicates per collecting method. The non-parametric incidence-based coverage estimator (ICE; Chazdon *et al.* 1998) and Michaelis-Menten Mean (MMMean) richness estimators were used to evaluate sample size adequacy (Colwell & Coddington 1994). ICE and MMMean richness estimators were chosen as they have performed well in studies with small sample sizes (Chazdon *et al.* 1998; Toti *et al.* 2000). When the observed rarefaction curves (S_{obs} (Mao Tao)) and the estimators (ICE and MMMean) converge closely at the highest observed richness, the richness estimates may be considered representative (Longino *et al.* 2002). Species richness (i.e. the total number of species (Magurran 2004) for this study is defined as the total number of species sampled across all sampling events) between treatments was compared using sample-based rarefaction curves that were rescaled by individuals, to adjust for differing densities of individuals (Gotelli & Colwell 2001). Species richness was compared by plotting the treatment rarefaction curves with their 95 % confidence intervals. If the confidence intervals overlapped, the differences were not significant at $p < 0.05$ (Colwell *et al.* 2004).

Species density and abundance of both beetles and spiders were determined for each treatment (high infestation, medium infestation, surrounded and pristine treatments). Species density is the number of species per specified collection area or unit (Magurran 2004) and for this study is defined as the number of species sampled during one sampling event using a defined sampling effort. To calculate species density and abundance for both spider and beetle species, the total number of species captured was pooled for the six sampling events for each of the treatments i.e. five replicates per collecting method. Spider species were pooled for the different collecting methods. Species density was summed for each treatment replicate and compared using ANOVA and post-hoc Tukey tests. Similarly for abundance, the number of individuals sampled was summed for each treatment replicate (five pitfall traps) in each sampling period and compared between treatments using ANOVA and post-hoc Tukey tests.

The beetle and spider assemblage structures within the four treatments were compared using ANOSIM. Common and rare species were weighted equally by double square-root transformation of the data before analysis and a Bray-Curtis similarity measure was used to calculate the similarity matrix.

The characteristic beetle and spider species (indicator species) were identified for each of the treatments using the Indicator Value Method (Dufrêne & Legendre 1997). The method assesses the degree (expressed as a percentage) to which each species fulfills the criteria of specificity (uniqueness to a site) and fidelity (frequency within that habitat type) for each habitat type compared with all other habitats. The higher the IndVal (indicator value) obtained, the higher the specificity and fidelity values for that species, and the more representative the species is of that particular habitat. Species with significant IndVals greater than 70 % (subjective benchmark; van Rensburg *et al.* 1999) are regarded as indicator species for the habitat in question (van Rensburg *et al.* 1999; McGeoch *et al.* 2002).

RESULTS

Ambient temperature measurements

Ambient temperature measurements did not differ significantly between the four treatments (ANOVA, $F_{3,16} = 0.12$, $p = 0.95$, $n = 48$), indicating a similar temperature across all four treatments.

Vegetation

Plant assemblage structure differed significantly between the treatments (Global R = 0.36, $p = 0.001$), but because the Global R is close to zero, the assemblages are close to being indistinguishable. Plant assemblage structure for heavily invaded sites was significantly different from pristine (Global R = 0.46, $p = 0.008$) and surrounded sites (Global R = 0.29, $p = 0.04$), but not significantly different from medium invaded sites (Global R = 0.26, $p = 0.09$). Plant assemblage structure of medium invaded sites was significantly different from both pristine (Global R = 0.32, $p = 0.008$) and surrounded sites (Global R = 0.53, $p = 0.008$). The plant assemblage structure of pristine and surrounded sites were significantly different (Global R = 0.46, $p = 0.008$).

Beetles and spiders

Seventy-two beetle species (2162 individuals) and 129 spider species (1051 individuals) were collected from the four treatments representing the gradient of *O. stricta* infestation at the study site. A total of 54 spider species were new locality records for KNP (Appendix 1).

For beetles, the observed richness (S_{obs}) converged closely with the richness estimators (ICE and MMMean) indicating a representative sample (Fig. 2a). However, the observed richness (S_{obs}) for the spider sample did not converge closely with the richness estimators indicating that the spiders were under sampled (Fig. 2b). Confidence intervals for both beetles and spiders overlapped indicating that differences in species richness between the four treatments were not significant at $p < 0.05$ (Figs. 3a & b). Beetle species density did not differ significantly across the treatments (ANOVA, $F_{3,16}$ = 1.88, $n = 20$, $p = 0.17$) while beetle abundance was significantly higher in heavily invaded sites when compared to pristine sites (ANOVA, $F_{3,16} = 3.59$, $n = 20$, $p = 0.04$) (Table 1). Spider species density (ANOVA, $F_{3,16} = 1.23$, $n = 20$, $p = 0.33$) and abundance (ANOVA, $F_{3,16} = 1.81$, $n = 20$, $p = 0.19$) did not differ significantly across the treatments (Table 1).

Although significant, the overall difference in the assemblage structure of beetles when compared between all four the treatments is small, suggesting that the assemblages in all four treatments are not distinguishable from one another (Global R = 0.19, p = 0.008). Heavily invaded assemblages were not significantly different from medium invaded assemblages (Global R = -0.08, p = 0.69) or from surrounded assemblages (Global R = 0.08, p = 0.17), but were significantly different from pristine assemblages (Global R = 0.32, p = 0.01). Medium invaded assemblages were significantly different from pristine assemblages (Global R = 0.27, p = 0.03) but not surrounded assemblages (Global R = 0.22, p = 0.07). Pristine assemblages and surrounded assemblages were significantly different (Global R = 0.44, p = 0.01). Overall spider assemblage structure did not differ significantly across the four treatments (Global R = 0.09, p = 0.15).

Interestingly, no beetle or spider species fulfilled the criteria for indicator species (IndVal ≥ 70 %) in any of the treatments. When including species with significant IndVal of above 60 % (i.e. lowering the subjective benchmark), two beetles (*Acmaeodera virgo* Boheman, 1860, IndVal = 60 %, $p < 0.05$ and *Philoserica vittata* Blanchard, 1850, IndVal = 60 %, $p < 0.05$) and one spider (*Runcinia flavida* (Simon, 1881), IndVal = 60 %, $p < 0.05$) were characteristic of pristine sites. Additionally, one spider species (*Natta chionogaster* (Simon, 1901), IndVal = 66.67 %, $p < 0.05$) was characteristic of the medium invaded sites.

Table 1. Species density and abundance of beetles and spiders collected in the Kruger National Park within a gradient of *Opuntia stricta* infestation. n = number of sampling sites, S = total species density (observed number of species) and N = total abundance. Means with no letters in common denote significant differences between treatments calculated at $p < 0.05$.

Treatment	Density mean ± SE	Abundance mean ± SE	n	S	N
Beetles	$F_{3, 16} = 1.88$, $p = 0.17$	$F_{3, 16} = 3.59$, $p = 0.04$			
High infestation	24.00 ± 2.02[a]	151.40 ± 26.36[a]	5	46	757
Medium infestation	22.00 ± 2.10[a]	112.60 ± 19.31[ab]	5	48	563
Surrounded	23.20 ± 2.40[a]	106.00 ± 17.01[ab]	5	47	530
Pristine	17.80 ± 1.39[a]	63.20 ± 9.97[b]	5	48	316
Spiders	$F_{3, 16} = 1.23$, $p = 0.33$	$F_{3, 16} = 1.81$, $p = 0.19$			
High infestation	24.60 ± 2.69[a]	59.20 ± 11.57[a]	5	64	296
Medium infestation	26.80 ± 3.37[a]	56.60 ± 11.30[a]	5	72	283
Surrounded	21.20 ± 1.59[a]	33.60 ± 2.56[a]	5	62	168
Pristine	27.20 ± 2.85[a]	58.80 ± 8.66[a]	5	75	294

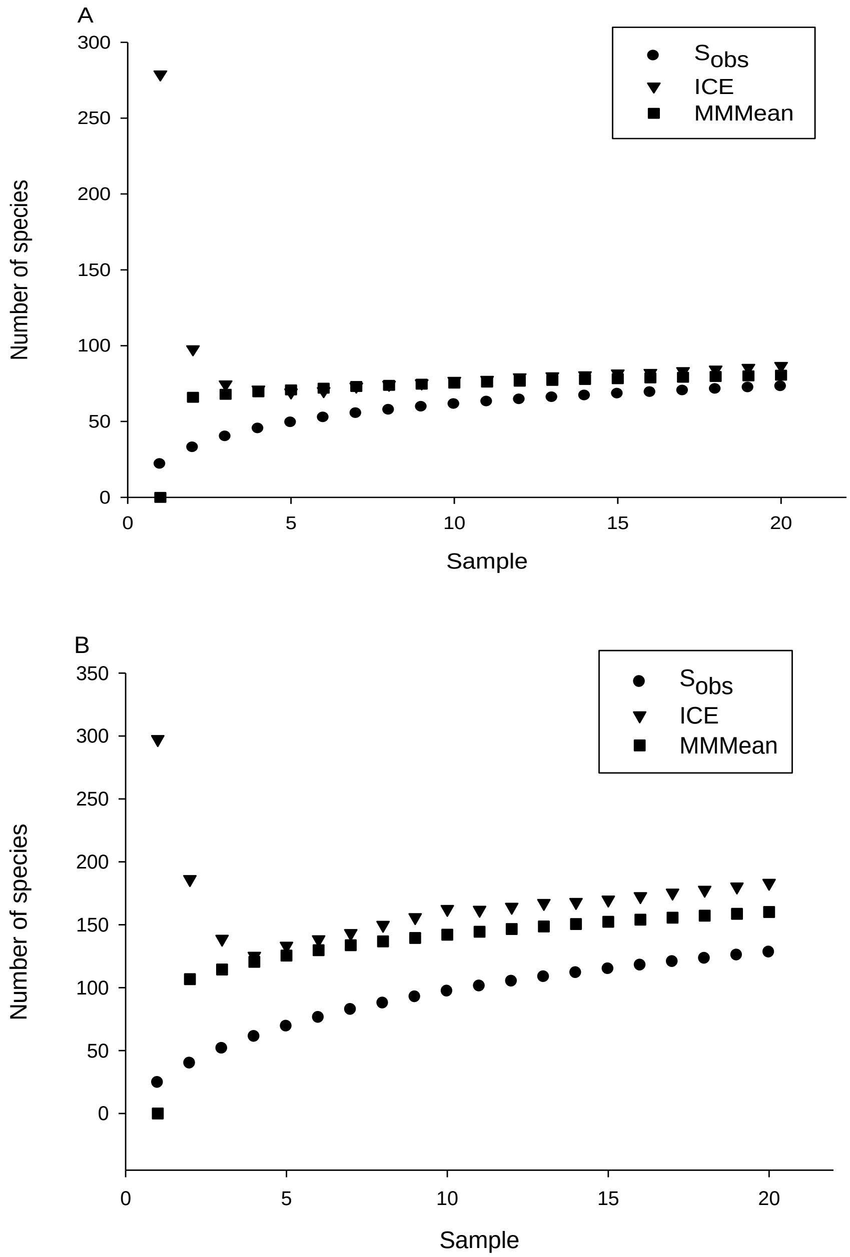

Fig. 2. Sample-based rarefaction curves indicating observed number of species (S_{obs} Mao Tao), incidence-based coverage estimator (ICE) and Michaelis-Menten Mean (MMMean) richness estimators, of beetles (a) and spiders (b) collected in *Opuntia stricta* invaded sites in the Kruger National Park.

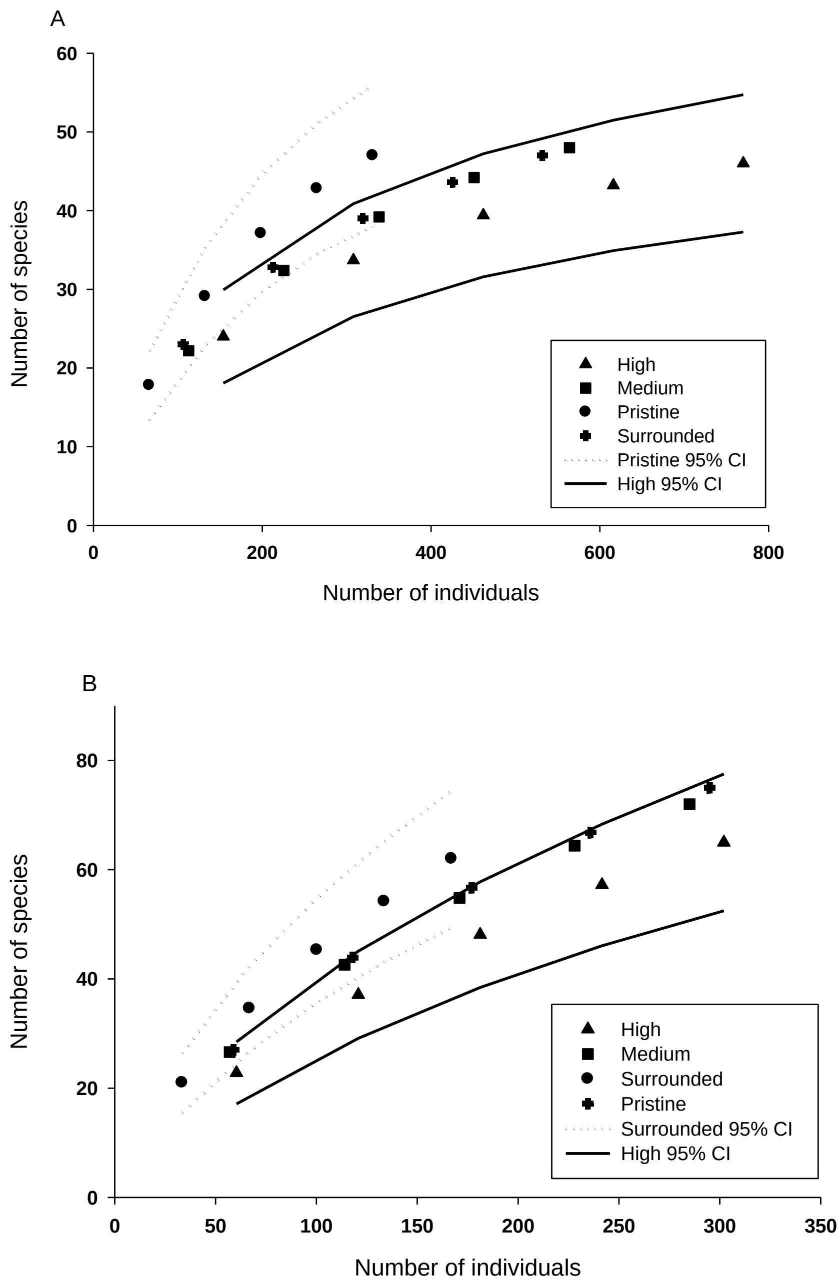

Fig. 3. Sample-based rarefaction curves indicating observed number of beetle species (a) and spider species (b) (S_{obs}) collected in *Opuntia stricta* invaded sites in the Kruger National Park. Species richness should be compared when the number of individuals is equal in all treatments (i.e. approximately 340 individuals for beetles; approximately 180 individuals for spiders). The finely dashed lines represent the 95 % confidence interval.

Where confidence intervals overlap, the differences in species richness are not significant at $p > 0.05$.

DISCUSSION

Invasion by *Opuntia stricta* does not appear to significantly affect beetle and spider species richness or density. These findings are in direct contrast to most other studies that have investigated the impacts of invasive plants on arthropod diversity across a variety of habitats; both within South Africa (Samways & Moore 1991; Samways *et al.* 1996; Steenkamp & Chown 1996; Samways & Taylor 2004; Coetzee *et al.* 2007) and elsewhere (Toft *et al.* 2001; Greenwood *et al.* 2004; Ernst & Cappuccino 2005; Bultman & DeWitt 2008). As with most other taxa (e.g. birds - Blackburn *et al.* 2004; fishes - Levin *et al.* 2006; amphibians - Maerz *et al.* 2005), changes in arthropod assemblages, due to biological invasion, are often associated with a change in body size distributions (Steenkamp & Chown 1996; Coetzee *et al.* 2007), a reduction in species richness (Gerber *et al.* in press) and a change in abundance values (French & Major 2004).

Variation in vegetation structure because of alien plant invasion has been cited as one of the principal causes of changes in arthropod assemblages (Standish 2004; Coetzee *et al.* 2007). Lower abundance and diversity of terrestrial arthropods is a result of simpler habitat structure and lower plant diversity in invaded sections (Greenwood *et al.* 2004). French & Eardley (1997), found minimal impacts in litter invertebrate assemblages in shrub land invaded by *Chrysanthemoides monilifera* (Asteraceae) when compared with native heath land of similar structure (i.e. height, canopy and leaf litter cover). While Mgobozi *et al.* (2008) cited the decrease of habitat heterogeneity in savanna in KwaZulu-Natal as the most likely cause of the reduction of spider species richness and abundance in patches of *Chromolaena odorata* (Asteraceae), a non-indigenous perennial shrub that reaches a height of 8-10 m. Although considered a transformer species (i.e. an invasive species that changes the character, condition, form or nature of ecosystems over a substantial area (Richardson *et al.* 2000)); the *O. stricta* density and infestation in KNP has decreased in size and has become patchy in nature (see Fig. 1) due to the effective biocontrol programme initiated in 1988 (Foxcroft pers. comm.). When compared to the impenetrable thickets associated with other South African savanna invaders such as *Prosopis glandulosa* (Fabaceae) and *Chromolaena odorata* (Asteraceae), the patchiness of the *O. stricta* infestation is probably one of the main factors contributing to the minimal impact on arthropod assemblages. In addition, the *O. stricta* infestation in the KNP does not dominate the tree canopy as other species such as the Australian acacias in the Fynbos or Grassland (e.g. Coetzee *et al.* 2007).

Research on *O. stricta* invasion in the KNP has shown a steady decrease in the size of the infestations and the number of cladodes per plant due to biological control. For example, Lotter (1996) reported 68 dense impenetrable clumps of *O. stricta* and Hoffmann *et al.* (1998a) found several plants with more than 150 cladodes. In this study, I found only a few dense stands of *O. stricta* (approximately 15) and no plants with more than 150 cladodes. *Dactylopius opuntiae* is mass reared under hothouse conditions and released throughout *O. stricta* infestations in and around KNP (Foxcroft & Hoffmann 2003). Indeed, from an *O. stricta* point of view, the biological control programme spanning the last 20 years has been highly successful at reducing the infestation levels of this species to feasible maintenance levels. Clearly, this study seems to support these successful management actions from an arthropod perspective, at least for spiders and beetles. Economically this is the point at which the follow up control is quickest and cheapest and biologically it is the point where biodiversity is least affected by *O. stricta*. KNP management has moved away from mechanical and herbicidal methods of control and relies now only on biological control, which is a more economically viable option (Foxcroft pers. comm.). Although the Level 3 TPCs are not yet operational due to the lack of data and clearly defined measurable outcomes, the results of this study will contribute to the broader understanding of the impacts of invasive alien species on biodiversity in KNP. Further research will be able to produce biodiversity thresholds of potential concern (bTCPs) which will address the negative impacts of alien species on biodiversity (Foxcroft 2008).

The lack of suitable indicator species for a given treatment further supports the result of no significant arthropod assemblage differences between the four treatments. Moreover, the Indicator Value concept developed by Dufrêne & Legendre (1997) to detect and monitor change in assemblages due to a change in environmental conditions currently offers little value to the KNP management when assessing the impacts of *O. stricta* infestations on biodiversity. This is true at least for spiders and beetles at the current *O. stricta* infestation levels.

Based on spider and beetle data spanning a full annual cycle, it seems that current *O. stricta* infestation does not have a significant effect on the species assemblages of these groups in the KNP. However, a study similar to this one conducted pre 1988, i.e. before the initiation of the biological control programme, would have been ideal to support this conclusion. Plant assemblage structure in the invaded treatments, at their current level of infestation, is very similar when compared with the pristine treatment. It is therefore likely that these similar structures provide similar habitats for beetles and spiders, which results in unchanged assemblages. The effectiveness of the biological control agents, *C. cactorum* and *D. opuntiae*, has curbed the densification of the *O. stricta* infestations (Hoffman 1998b) which, in all likelihood has contributed to the arthropod assemblages showing no significant differences among the infestation treatments.

Despite the vigour of management policies, invasive alien organisms have become permanent fixtures in protected areas in many parts of the world (Usher 1988; Lonsdale 1999). The same can be said of KNP, without any permanent eradication options most alien invasive organisms, including *O. stricta*, will persist. However, this study clearly indicates that, at least from a spider and beetle perspective, these management actions should continue in order to uphold the KNP's alien impact objectives in the most economically viable manner and further mitigate the impacts of *O. stricta*. Nevertheless, to add more confidence to the alien impact objective, the effect of *O. stricta* on other arthropod groups, such as ants, pollinators and other herbivorous arthropod taxa should be examined further.

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Appendix 1. The total number of beetles and spiders, listed per family, collected in the Kruger National Park, South Africa in four different levels of *Opuntia stricta* infestation. Spider species names marked with ∗ represent new records for the region.

Species	**Heavy infestation**	**Medium infestation**	**Surrounded**	**Pristine**
Order: Coleoptera				
Buprestidae				
Acmaeodera luteopicta Fåhraeus, 1851				1
Acmaeodera virgo Boheman, 1860				4
Carabidae				
Abacetus auspilatus Peringuey				1
Anthia thoracica (Thunberg, 1784)	17	17	13	7
Aulacoryssus pavoninus (Gerstaecker,1866)	1	1	11	
Callistoides pulchellus (Boheman,1848)				1
Carabidae sp. 1			1	
Carabidae sp. 2			2	
Carabidae sp. 3		1	7	4
Chlaenius marginicollis Boheman,1848		1	1	
Crepidogastrini cicatricosa Jeannel, 1949	5	16	8	
Dromica simplex (Bates, 1878)	6	4		

Graphipterus fasciatus distinctus Peringuey, 1899	57	27	15	3
Graphipterus griseus Latreille, 1802				2
Megacephala regalis Boheman, 1848				1
Pachydinodes bipustulatus Boheman, 1848	1		10	3
Polyhirma graphipteroides Guérin-Méneville, 1845		1		
Polyhirma alveolata Brime, 1844				1
Tefflus carinatus Klug, 1853	1	3		1
Thermophilium homoplatum Lequien, 1832	45	19	20	5
Cerambycidae				
Crossotus stypticus Pascoe, 1869				1
Chrysomelidae				
Aspidimorpha tecta Boheman,1854				1
Curculionidae				
Brachycerus congestus Gerstäcker, 1855				1
Brachycerus sp. 1	3			
Calodemas sp. 1	11	4	7	2
Cyclominae sp. 1	3	3	2	2
Hoplitotrachelus spinifer Schoenherr, 1848		1		
Microcerus costalis Fåhraeus, 1871	1	2	4	

Microcerus fallax Fåhraeus, 1871	5	2	4	4
Spartecerus sp. 1	11	11	3	4
Histeridae				
Hister tropicus Paykull, 1811	3	10	6	
Pactolinus gigas (Paykull, 1811)				1
Hybosoridae				
Hybosorus CF *rufieofnis*		4	2	
Meloidae				
Ceroctis delagoensis	8	46	7	37
Scarabaeidae				
Adoretus CF *ictericus*	2			
Adoretus CF *punctipennis*	1			
Adoretus tessulatus Burmeister,1855	3	1	2	2
Anachalcos convexus Boheman, 1857	154	71	44	8
Copris amyntor Klug, 1855	11	6	3	6
Copris elphenor Klug, 1855	1	3	3	1
Copris mesacanthus Harold, 1878	50	30	12	25
Garetta nitens (Olivier 1789)	10	9	9	2

Gymnopleurus ignitus Klug, 1855	6	2	20	
Gymnopleurus sp. 1		1	1	1
Heteronychus arator Burmeister, 1847				1
Leucocelis amethystina (McLeay,1838)	2	2		
Onitis crenatus Reiche, 1847	2		2	
Onitis uncinatus Klug, 1855			1	
Onthophagus tersidorsis D'Orbigny, 1902	2	7	5	
Onthophagus bicavifrons D'Orbigny, 1902				5
Onthophagus gazella Fabricius, 1787			3	
Onthophagus sp. 1	41	17	80	9
Phalops ardea Klug, 1855			1	
Philoserica vittata Blanchard, 1850				8
Pseudolinteria cincticollis			1	
Scaptobius sp. 1	2	1	2	5
Scarabaeus nigroaeneus Boheman, 1857	29	26	53	3
Sisyphus costatus Thunberg, 1818	2	1	3	
Trochallus sp. 1	3	2		1
Tenebrionidae				
Amachla sp. 1	108	113	69	21
Anomalipus carinatus Oertzen, 1897	94	36	51	41
Anomalipus elephas Fåhraeus, 1870	2	2		1

Aspidomorpha prona	3	1	1	4
Distretus amplipennis Fåhraeus, 1870	14	5	1	6
Drosochirini sp. 1	3	4	2	
Drosochirini sp. 2	15	1	1	2
Micranterus scaberrimus Fairmaire	2	5	1	1
Psammodes striatus Fabricius, 1775		2		
Serrichora fahraei	2	7	2	6
Somaticus CF *angulatus*	1	2		4
Strongylini sp. 1	1			3
Zophisini sp. 1	12	27	29	55
Zophisini sp. 2		2	1	7
Trogidae				
Omorgus squalidus Olivier, 1789	1	1	4	
Total Coleoptera/treatment	**757**	**560**	**530**	**315**
Total Coleoptera	**2162**			

Order: Araneae				
Agelena sp. 1*		2		
Benoitia ocellata (Pocock, 1900)*		1		
Araneidae				
Argiope australis (Walckenaer, 1805)	1			
Argiope lobata (Pallas, 1772)*			1	
Caerostris sexcuspidata (Fabricius, 1793)	1	1		1
Chorizopes sp. 1*			1	1
Cyphalonotus larvatus (Simon, 1881)		1		
Cyrtophora citricola (Forskål, 1775)	4	3	1	1
Hypsosinga lithyphantoides Caporiacco, 1947*	1	1		1
Isoxya stuhlmanni (Bösenberg & Lentz, 1895)	2	1		
Neoscona blondeli (Simon, 1885)	2	1	1	
Prasonica sp. 1				
Pararaneus sp. 1*			1	
Singa albodorsata Kauri, 1950				1
Caponiidae				
Caponia natalensis (O.P.-Cambridge, 1874)		2		2

Corinnidae				
Castianeira sp. 1		2		1
Copa flavoplumosa Simon, 1885*	1			1
Corinnomma semiglabrum (Simon, 1896)*		1		
Messapus sp. 1*	2			
Merenius alberti Lessert, 1921	2	1	2	
Ctenidae				
Anahita sp. 1				1
Ctenus gulosus Des Arts, 1912	2	2	2	1
Cyrtaucheniidae				
Ancylotrypa barbertoni (Hewitt, 1913)				1
Ancylotrypa brevipalpis (Hewitt, 1916)*	9	6	1	
Ancylotrypa sp. 1*	2			2
Ancylotrypa sp. 2*	1			
Ancylotrypa sp. 3*	1			
Dictynidae				
Mashimo leleupi Lehtinen, 1967			1	

Eresidae				
Adonea sp. 1*				1
Gnaphosidae				
Aphantaulax inornata Tucker, 1923	1	2		
Asemesthes ceresicola Tucker, 1923*	2	8	6	21
Asemesthes numisma Tucker, 1923			1	
Asemesthes purcelli Tucker, 1923		1		
Asemesthes sp. 1*	12	10	7	22
Camillina corrugata (Purcell, 1907)		2	2	3
Drassodes masculus Tucker, 1923*	4	1	1	
Drassodes splendens Tucker, 1923*		1	5	4
Drassodes sp. 1			1	
Pterotricha auris (Tucker, 1923)	4	6	2	4
Setaphis arcus Tucker, 1923	3	4		13
Setaphis browni (Tucker, 1923)		1		
Xerophaeus sp. 1		4		
Zelotes oneili (Purcell, 1907)*			1	
Zelotes tuckeri Roewer 1951*	3	4	7	1
Zelotes ungulus Tucker, 1923*		1		
Zelotes sp. 1		1		

Idiopidae				
Segregara mossambicus (Hewitt, 1919)*		1		
Lycosidae				
Arctosa sp. 1				1
Geolycosa sp. 1	5	4	5	3
Hippasa australis Lawrence, 1927	8	10	11	9
Hogna sp. 1	13	20	4	12
Hogna transvaalica (Simon, 1898)	67	45	19	39
Lycosa sp. 1			1	
Lycosidae sp. 1	58	47	12	34
Ocyale sp. 1				1
Pardosa sp. 1*	2	3	4	9
Pardosa sp. 2*	5	1	5	4
Trabea sp. 1				1
Miturgidae				
Cheiracanthium furculatum Karsch, 1879			1	
Cheiramiona krugerensis Lotz, 2002	1		4	1

Oxyopidae				
Oxyopes falconeri Lessert, 1915*	1		1	2
Oxyopes hoggi Lessert, 1915*	1	2		
Oxyopes jacksoni Lessert, 1915				1
Oxyopes longispinosus Lawrence, 1938	1			2
Oxyopes pallidecoloratus Strand, 1906			1	1
Oxyopes sp. 1	1	1	1	2
Oxyopes sp. 2				1
Peucetia sp. 1	1			2
Palpimanidae				
Diaphorocellus biplagiatus Simon, 1893			2	1
Palpimanus transvaalicus Simon, 1893	5	4	3	2
Philodromidae				
Hirriusa variegata (Simon, 1895)			3	2
Philodromus sp. 1	1	1	1	
Suemus punctatus Lawrence, 1938	1	2	3	4
Pholcidae				
Smeringopus natalensis Lawrence, 1947				1

Spermophora sp. 1*				1
Pisauridae				
Afropisaura rothiformis (Strand, 1908)	1		1	2
Euprosthenops australis Simon, 1898	5		2	
Euprosthenopsis pulchella (Pocock, 1902)*	1	2	1	1
Maypacius bilineatus Pavesi, 1895*		1		1
Prodidomidae				
Prodidiomus sp. 1*	1			
Salticidae				
Aelurillus sp. 1		1		
Baryphas ahenus Simon, 1902	2		2	3
Evarcha sp. 1	2	1		3
Hyllus argyrotoxus Simon, 1902*	13	5	9	5
Hyllus treleaveni Peckham & Peckham, 1902*	2	3	1	
Langelurillus sp. 1*	2	1		2
Langona sp. 1*			1	
Mexcala sp. 1*		1		1
Natta chionogastra (Simon, 1901)*		8	4	
Stenaelurillus sp. 1*	5	1		4

Stenaelurillus sp. 2*	2		1	7
Stenaelurillus sp. 3*		2		2
Stenaelurillus sp. 4*	4	3	1	2
Thyene coccineovittata (Simon, 1885)	1	1		3
Thyenula sp. 1*	1	1	1	
Scytodidae				
Scytodes constellata Lawrence, 1938*		1		1
Scytodes trifoliata Lawrence, 1938*				1
Sicariidae				
Loxosceles spiniceps Lawrence, 1952	6	9		4
Sparassidae				
Olios correvoni Lessert, 1921	2	1	1	
Olios machadoi Lawrence, 1952*	6	3	2	
Olios tuckeri Lawrence, 1927*		2		
Panaretella sp. 1		1		2
Panaretella zuluana Lawrence, 1937*	2			
Tetragnathidae				

Leucauge festiva (Blackwall, 1866)	2			
Theraphosidae				
Augacephalus breyeri (Hewitt, 1919)			1	2
Ceratogyrus bechuanicus Purcell, 1902	1			
Ceratogyrus dolichocephalus Hewitt 1919	1			
Harpactirella flavipilosa Lawrence, 1936*	1	5	3	3
Idiothele nigrofulva (Pocock, 1898)		1	2	
Pterinochilus lugardi Pocock, 1900*		1	1	
Theridiidae				
Argyrodes convivans Lawrence, 1937	1			
Chorizopella tragardhi Lawrence, 1947*			1	
Dipoena sp. 1*	1		1	1
Euryopis sp. 1	1	3	1	2
Latrodectus geometricus C.L. Koch, 1841		1		
Thomisidae				
Diaea puncta Karsch, 1884*				1
Heriaeus fimbriatus Lawrence, 1942*	1		1	1
Monaeses pustulosus Pavesi, 1895		1	2	

Monaeses quadrituberculatus Lawrence, 1927	1			1
Runcinia flavida (Simon, 1881)				3
Simorcus cotti Lessert, 1936	1			
Stiphropus sp. 1*				1
Thomisops pupa Karsch, 1879				1
Thomisus daradioides Simon, 1890			1	
Thomisus granulatus Karsch, 1880		2	2	1
Xysticus lucifugus Lawrence, 1937*				1
Uloboridae				
Miagrammopes longicaudus (O.P.-Cambridge, 1882)		1		
Zodariidae				
Capheris decorata Simon, 1904	2	5	1	6
Cydrela schoemanae Jocqué, 1991	2	2		6
Cydrela sp. 1		1		
Ranops caprivi Jocqué, 1991		1	1	
Total Araneae /treatment	**304**	**284**	**170**	**293**
Total Araneae	**1051**			
Total arthropods	**3213**			

CHAPTER 4

GENERAL DISCUSSION

The influx of non-native species from human activities has shaped many biological communities and will continue to do so in the near future (Mack *et al.* 2000). Invasion biologists are tasked with the enormous responsibility of identifying impacts posed by biological invasion, identifying future invaders and preventing their dispersal and establishment. Biological invasion of protected areas is also of major concern as these invasions are often the primary threat to biodiversity and undermine the core principles of conservation, which is to maintain formally protected areas. Kruger National Park (KNP) is no exception as invasive alien plants are the greatest threat to biodiversity ahead of traditional threats such as fragmentation and poaching (Foxcroft & Freitag-Ronaldson 2004). These protected areas are becoming more isolated and are often islands of relatively intact ecosystems surrounded by land use practices often incompatible with biodiversity conservation (Foxcroft *et al.* 2007). The extent at which differing land use practices outside the protected areas impact on the functioning of ecosystems within such areas is dependent on various socio-economic factors and the geography of the region (Pollard *et al.* 2003). Besides the many edge effects associated with the surrounding land use practices, rivers and roads are major conduits of invasive alien organisms (Pŷsek & Prach 1994). Consequently, managing invasive alien organisms in these protected areas is a growing challenge (Foxcroft *et al.* 2008). Successful management practices depend on prevention, early detection, management, eradication, containment and control (Wittenberg & Cock 2005).

As a result of rapidly decreasing global biodiversity (Pimm & Raven 2000; Purvis & Hector 2000), calls have increasingly been made to create an inventory of global species diversity (Stork & Samways 1995). This implies protecting terrestrial arthropods, a group that comprises 80 % of the Earth's species and which regulate many important processes fundamental to ecosystem functioning (Wilson 1987). As a signatory to the Convention on Biological Diversity in 1995, South Africa is obliged to retain as much of its biodiversity as possible. Inventories are therefore vitally important for the conservation of the region's biodiversity (Scholtz & Chown 1993; van Rensburg *et al.*

2004; Driver *et al.* 2005; Nel *et al.* 2007). In order to create inventories, standardized collecting methods need to be formulated and assessed whether they complement one another. Therefore, the primary aim of Chapter 2 was to assess the degree to which different methods complement each other in terms of the species they capture. The methods (pitfall trapping, leaf litter sifting and active searching) presented are considered to be ideal for collecting in a savanna habitat transformed by *O. stricta* infestation and all three methods are necessary in order to comprehensively sample spider diversity. All three methods did however, under-sample to some extent and additional sampling events are required for all methods. Although not a specified objective, the accompanying spider species list that was generated will add valuable data to the South African National Survey of Arachnida (SANSA) database. In addition, the 54 new spider locality records will also be a useful contribution for updating the invertebrate records for the KNP.

The impacts of invasive alien plants have been shown to be detrimental to native biodiversity in several studies (e.g. Toft *et al.* 2001; Herrera & Dudley 2003; Greenwood *et al.* 2004; Ernst & Cappuccino 2005). The primary aims of this study were to assess the impacts of *O. stricta* infestation on beetle and spider assemblages and to identify beetle and spider species that were characteristic as indicated that spider species richness of each *O. stricta* infestation level. However, in this study, the results from Chapter 3 indicate no significant differences in beetle and spider species richness, species density and assemblage structure in sites that were invaded by *O. stricta* when compared to sites that had not been invaded. In addition, none of the beetle or spider species that were collected could be considered a good indicator species of any of the four treatments, further indicating that the *O. stricta* infestation had no significant impact on arthropod assemblages. The similarity of the vegetation structure between the treatments is probably a major contributing factor to this result. The ongoing biological control programme initiated by the KNP in 1988 has played an important role in reducing the patch size of the *O. stricta* infestation and the size of the plants. With this result in mind, the biological control programme needs to be continued in order to further mitigate the impacts of *O. stricta* on arthropod assemblages in the KNP. The result is a major contribution towards addressing one of KNP's invasive alien species objectives, which is stated as follows:

"To anticipate, prevent entry, eradicate or minimize the influence of non-indigenous organisms so as to maintain the integrity of native biodiversity" and more specifically: *"To determine the impact of all invasive alien species in KNP in terms of biodiversity: structure, composition and function"* (Foxcroft & Freitag-Ronaldson 2004).

TPCs provide an ideal framework for assessing change in ecosystem structure, function and composition at specified temporal and spatial scales (Foxcroft & Richardson 2003). The TPCs proposed for alien invasive organisms and their impacts on biodiversity are not yet operational due to a variety of reasons discussed in Chapter 1. The results from this project however, do provide insights into the impacts of *O. stricta* invasion on beetle and spider assemblages within KNP. Further thought is required on how to incorporate the results of this study into practical management tools, which are in this case the biodiversity thresholds of potential concern (bTPCs). These bTPCs will then be able to express impacts in terms of biodiversity loss due to alien species in the KNP system.

Although the study provides valuable information for KNP's invasive alien species objectives, one limitation has been identified which concerns the size of the study area and the number of replicates. In terms of the experimental design, the study area is limited by the size of the current *O. stricta* infestation, which has decreased in size and density since the introduction of the two biological agents (Foxcroft pers. comm.). The study area selected represents the main concentration of the *O. stricta* infestation in KNP and while other infestations exist, they are significantly smaller. Although reduced, the current size of the *O. stricta* infestation represents a real-world scenario, and is considered the most problematic of the 370 invasive plant species identified in KNP (Foxcroft *et al.* 2007).

With the results of the study in mind and to further ascertain the impacts of *O. stricta* on arthropod assemblages additional research is required. These may include:

- As shown by the spider species accumulation curves, further sampling is required for all three methods (pitfall trapping, leaf litter sifting and active searching) in order to adequately sample spider species richness.

- The impact of *O. stricta* on other arthropod assemblages needs to be determined. Ants would be an ideal group to work with, as they have been shown to be good indicators of habitat change (Andersen & Majer 2004).
- Further monitoring of the *O. stricta* infestation is required to ascertain how large the current infestation is, so that the resources allocated to biological control can be either increased or decreased.
- Additional work is required to determine whether the current *O. stricta* infestation has any effect on ecosystem processes such as nutrient cycling, erosion patterns and ground water cycling.
- Further collaboration is required on how to integrate the results of this study into formulating Level 3 TPCs or biodiversity TPCs.

In conclusion, the major finding of this study is that invasion by *O. stricta* may have limited impacts on arthropod diversity in the KNP. This appears to be dependent on the extent to which *O. stricta* alters the vegetation structure and the density of the infestation. The other major conclusion is that invasive species can be maintained at levels (using appropriate management) where their impact on arthropod diversity is limited. However, the impact of non-native species on native biodiversity and ecosystem processes is still a major concern in South Africa and across the globe. The importation of non-native species is accelerating and we are increasingly faced with a future of a homogenized biosphere. With limited resources at hand, it is important that emerging invaders be identified early enough in order to minimize their impact on biodiversity and the ecosystem services derived from it. Successful management practices depend on prevention, early detection, management, eradication, containment and control. Protected areas are also faced with invasion by non-native species as human populations increasingly encroach on their borders. Management practices should favour the long-term sustainability and health of these protected areas, which may be dramatically altered by the invasion of non-native species.

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