Assessing local scale impacts of *Opuntia stricta* (Cactaceae) invasion on beetle and spider diversity in Kruger National Park, South Africa

M.P. Robertson[1*], K.R. Harris[1], J.A. Coetzee[2], L.C. Foxcroft[3,4], A.S. Dippenaar-Schoeman[5,6], B.J. van Rensburg[1]

[1]*Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa*

[2]*Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa*

[3]*Conservation Services, South African National Parks, Private Bag X402, Skukuza, 1350 South Africa*

[4]*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, 7602 South Africa*

[5]*Plant Protection Research Institute, Agricultural Research Council, Private Bag X134, Queenswood, 0121 South Africa*

[6]*Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028 South Africa*

Received 30 August 2010. Accepted 12 October 2010

There is a paucity of studies examining direct impacts of introduced alien species on biodiversity, a key need for motivating for alien species control in conservation areas. The introduced prickly pear (*Opuntia stricta*) has invaded some 35 000 ha of Kruger National Park. We investigated the effect of *O. stricta* on beetle and spider species assemblages in the Skukuza region of Kruger National Park. We used unbaited pitfall traps over a 12-month period in four treatments of varying *O. stricta* density. Species richness, species density and abundance of beetles and spiders were compared. A total of 72 beetle and 128 spider species were collected. Species richness and species density for beetles and spiders did not differ significantly across the four treatments. Assemblages for spiders did not differ across treatments but beetle assemblages were significantly different from uninvaded control sites. This study suggests that the current density of *O. stricta* does not significantly affect spider species richness, density or assemblages but that beetle assemblages are significantly affected.

Key words: **Araneae, arthropods, Coleoptera, invasion impacts, invasive plants, non-native, *Opuntia stricta*.**

INTRODUCTION

Patterns of invasions of flora and fauna 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 (van Wilgen 2004). Both globally and in South Africa, the impacts of invasive species, especially plants, on invertebrate diversity is still poorly understood (Samways & Moore 1991; Steenkamp & Chown 1996; French & Major 2001; Samways & Taylor 2004; Gratton & Denno 2005; Coetzee *et al.* 2007). It is important to quantify these impacts because invertebrates make a large contribution to global species diversity and are important in regulating many fundamental processes in most biomes throughout the world (Wilson 1987).

Invertebrates have been 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 alien plants. Bio-indicators can be classified into three categories: biodiversity, environmental and ecological indicators (McGeoch 1998). A biodiversity indicator provides information on the presence of a set of other species in an area, while environmental indicators directly show change in the state of the abiotic environment. Spiders (Araneae) constitute a highly diverse group and their trophic position and mobility suggest that they are ideal candidates for use as bio-indicators (Churchill 1997). Several studies have already advocated the use of spiders as indicators of habitat quality and

*Author for correspondence. E-mail: mrobertson@zoology.up.ac.za

change in a variety of habitats (Pétillon *et al.* 2005; Scott *et al.* 2006; Foord *et al.* 2008; Mgobozi *et al.* 2008). Dung beetles (Scarabaeidae) and ground beetles (Carabidae) are also considered 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 & Niemelë 2003; Coetzee *et al.* 2007). Pearce & Venier (2006) advocated using both spiders and ground beetles to evaluate the impact of habitat fragmentation and the creation of forest edges.

Within the Kruger National Park (KNP), which is considered the flagship reserve in South Africa's protected area network (Carruthers 1995), invasive alien plants have been identified as one of the most pressing threats to biodiversity (Foxcroft & Richardson 2003). *Opuntia stricta* var. *dillenii* (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), while in total 66 000 ha are required for surveillance and containment. 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) (Volchansky *et al.* 1999). Both have played a major role in managing the weed (Foxcroft & Hoffmann 2000) and the density of the weed appears to have declined from what it was when the programme was initiated (Lotter 1996; Hoffmann *et al.*1998b).

Invasive organisms require long-term management programmes in protected areas in many parts of the world (Usher 1988; Lonsdale 1999). The population of a particular invasive organism needs to be managed to a level at which it has as little impact on biodiversity and ecosystem services as possible. Quantifying these impacts on biodiversity and understanding the level of management required to reduce the impacts to an acceptable level requires carefully designed studies. The management of alien invasive organisms in KNP is based on the concept of Thresholds of Potential Concern (TPCs) (Foxcroft 2009). 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: Level 1 TPCs target new or potential invasions or incursions within the KNP; Level 2 TPCs target increases in the distribution of alien species already in the KNP; 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). If different densities of *O. stricta* result in different impacts on beetle and spider assemblages, then this would provide some insights into density related impacts (Level 3 TPCs) and possibly inform the selection of appropriate thresholds.

The key objective of the KNP's alien species management and monitoring programme is to minimize the influence of non-indigenous organisms on native biodiversity. However, little is known about the effects of *O. stricta* invasion on arthropod assemblages and whether the current density of *O. stricta* can be considered to be having an impact on these assemblages (Harris 2009).

The aims of this study were: 1) to assess the impact of different densities of *O. stricta* on beetle and spider assemblages; 2) to determine whether current densities of *O. stricta* can be considered to be having an impact on beetle and spider diversity; 3) to identify beetle and spider species that are characteristic of each *O. stricta* density class and that could be used as indicator species for monitoring invasive plant impacts; 4) to determine whether impacts of *O. stricta* on beetles and spiders were confined only to patches of *O. stricta* or whether they were also present outside the patches in areas where the plant was not present.

METHODS

Study area

The KNP is situated on the eastern side of the Limpopo and Mpumalanga provinces of South

Table 1. Comparison of beetle and spider species density and abundance collected across a gradient of *Opuntia stricta* invasion density. *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 ± S.E.	Abundance mean ± S.E.	*n*	*S*	*N*
Beetles	$F_{3,16} = 1.88$, $P = 0.17$	$F_{3,16} = 3.59$, $P = 0.04$			
High	24.00 ± 2.02^{a}	151.40 ± 26.36^{a}	5	46	757
Medium	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
Control	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	24.60 ± 2.69^{a}	59.20 ± 11.57^{a}	5	64	296
Medium	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
Control	27.20 ± 2.85^{a}	58.80 ± 8.66^{a}	5	75	294

Africa and is bordered by Mozambique to the east. The park falls within the savanna biome (Scholes 1997) and covers a surface area of 1.9 million ha. The climate is subtropical and rainfall varies from 400 mm in the north to 700 mm in the south. Fieldwork was conducted in the Skukuza region of the KNP, South Africa (25°00′S 31°58′E), in the Sabie-Crocodile thorn thicket habitat type (Gertenbach 1983), as this region has been most heavily invaded by *O. stricta* (Foxcroft *et al.* 2007). 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 understorey vegetation.

Experimental design

In order to compare the effect of *O. stricta* density on beetle and spider assemblages, four different treatments, containing five replicates each, were selected to represent a gradient *O. stricta* density. Treatments were selected according to the size (i.e. ground cover) and density 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 area invaded in the study site, it was not possible to place the replicates further apart. The four treatments included high density, medium density, surrounded and an uninvaded control. The high treatment consisted of *O. stricta* patches with dense continuous cladodes covering a ground surface area larger than 100 m^2. The medium treatment consisted of *O. stricta* patches with dense continuous cladodes covering a ground surface area between 18 and 100 m^2. The surrounded treatment consisted of areas that were surrounded by *O. stricta* patches, but contained very few *O. stricta* plants. These areas covered a ground surface area of larger than 1 m^2 and were characterised by having a lower overall vegetation cover than any of the other treatments. This treatment was selected due to the patchy nature of *O. stricta.* We wanted to determine whether any possible impacts of *O. stricta* on beetles and spiders were confined only to patches or whether they were also present outside the patches. Finally, the control consisted of sites where *O. stricta* had not invaded and were at least 50 m away from other treatments and covered a ground surface area larger than 100 m^2 (Table 1). Sampling of beetles and spiders was conducted bimonthly for 12 months between 2005 and 2006 (i.e. six sampling events), commencing in July 2005 and ending May 2006.

Beetle and spider sampling

During each sampling event, beetles and spiders were collected using pitfall traps. Spiders were additionally sampled using leaf litter sifting and active searching methods.

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. Traps

were covered with a steel mesh grid, a novel method 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 placed randomly at two locations within each replicate and all leaf litter was sifted through a 5 × 5 mm mesh.

Active searching. Two 1 m^2 quadrats were randomly placed within each replicate on each sampling event. In each replicate, all habitats suitable for spiders (including the ground, plants, rocks and fallen logs) were searched for 15 minutes (between 08:00 and 16:00). To prevent any collecting bias, all active searching was conducted by one person. Spiders were identified to family level, and then where possible to species level. Spider voucher specimens are housed in the National Collection of Arachnida at the ARC-Plant Protection Research Institute, South Africa. Beetles were identified to species level where possible and beetle voucher specimens are housed at the Ditsong National Museum of Natural History, South Africa.

Vegetation sampling

Vegetation structure and species composition for each of the replicates was sampled during winter (August 2006) and summer (March 2007). In each replicate, a 100 m^2 plot was placed in the centre of the *O. stricta* patch. Species composition, percentage cover and plant height was recorded for each species in each of eight 1 m^2 quadrats that were laid out on the inner edge of the 100 m^2 plot (Fig. 1). To quantify the extent of *O. stricta* surrounding the quadrats, four 10 m line transects were extended outwards from the corners of each 100 m^2 plot at a 45° angle and four 10 m transects were extended from the centre of the boundary of the 100 m^2 plot at a 90° angle (Fig. 1). Each line transect was divided into 50 cm segments and the presence or absence of *O. stricta* was recorded in each segment. The total number of *O. stricta* plants per replicate was calculated by summing the presences across the eight transects of each replicate. As *O. stricta* was only present in the high, medium and surrounded treatments, this analysis was not conducted for the control.

Data analysis

Beetles and spiders. Sample-based rarefaction curves were compiled for the total number of beetles and spiders collected in the study to establish sampling-representavity using the analytically calculated S_{obs} (Mao Tao) of EstimateS V7.5 (Colwell 2005). For both spiders and beetles, the total number of samples was 120 (i.e. four treatments by five replicates per treatment on six sampling occasions = 120 samples). 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 can be considered to be 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 account 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

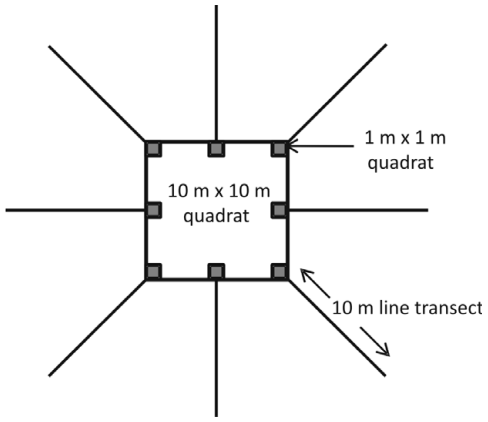

Fig. 1. Sampling design used to quantify vegetation composition in each replicate of the four treatments. A 10 m × 10 m quadrat (large square) was measured out and contained eight 1 m × 1 m quadrats (grey squares). Eight 10 m line transects (black lines) radiated out from the edge of each of the 1 m × 1 m quadrats. The line transect analysis was not conducted for the control.

and spiders were determined for each treatment (high, medium, surrounded and control). Species density is the number of species per specified collection area or unit (Magurran 2004). To calculate species density and abundance for both spider and beetle species, the total number of species captured across the six sampling events was pooled generating a total of 20 samples (i.e. four treatments with five replicates per treatment = 20 samples). Spider species data were pooled for the three 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.

Analysis of similarity (ANOSIM), implemented in the PRIMER 5.2.0 software package (Clarke & Warwick 2001), was used to compare beetle and spider assemblages across the four treatments (high, medium, surrounded, control). 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. ANOSIM generates a Global *R* statistic which can be used to quantify the similarity of assemblages being compared. The closer a significant Global *R* statistic is to one, the more distinct the differences are between the assemblages that are being compared. Pairwise tests are used to compare similarity of assemblages between pairs of treatments and give an *R* statistic that is interpreted in the same way as the Global *R* statistic. The similarities of the beetle and spider assemblages of each replicate were visualized using non-metric multidimensional scaling (NMDS) plots (Clarke & Warwick 2001).

The characteristic beetle and spider species (indicator species) were identified for each of the treatments using the Indicator Value Method (Dufrêne & Legendre 1997), calculated using the Labdsv package in R (R development core team, 2011). The method assesses the degree (expressed as a percentage) to which each species fulfils 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 indicator value (IndVal) obtained, the higher the specificity and fidelity values for that species, and the more representative the species is of that particular habitat (or treatment). Species with significant IndVals greater than 70% (subjective benchmark; van Rensburg *et al.* 1999) can be regarded as indicator species for the habitat in question (van Rensburg *et al.* 1999; McGeoch *et al.* 2002).

Vegetation. Cover estimates for plants were averaged over the two sample periods (August 2006 and March 2007). The mean cover of plants that were less than one metre in height was compared across treatments using an analysis of variance (ANOVA). As these cover values were recorded as percentages they were arcsine transformed prior to analysis (Crawley 2007). A Tukey test was then used to compare between treatments. The total number of *O. stricta* plants recorded along the transects was compared across treatments using an ANOVA.

Plant species assemblages (of both *O. stricta* and natural vegetation) of the four treatments were compared using an ANOSIM. 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.

RESULTS

Beetles and spiders

Seventy-two beetle (morpho) species (2162 individuals) and 128 spider (morpho)species (1051 individuals) were collected from the four treatments representing the gradient of *O. stricta* density at the study site (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). Given that spiders are a hyperdiverse group leading to high levels of spatial and temporal turnover in assemblage structure, this is a common problem in studies focusing on spider surveys (Coddington *et al.* 1996). Confidence intervals for both beetles and spiders overlapped indicating that differences in species richness among the four treatments were not significant (Fig. 3a,b). Beetle species density did not differ significantly across treatments (ANOVA, $F_{3,16} = 1.88$, $n = 20$, $P = 0.17$). Beetle abundance was significantly higher in heavily invaded sites compared to control sites (ANOVA, $F_{3,16} = 3.59$, $n = 20$, $P = 0.04$) (Table 1). Spider

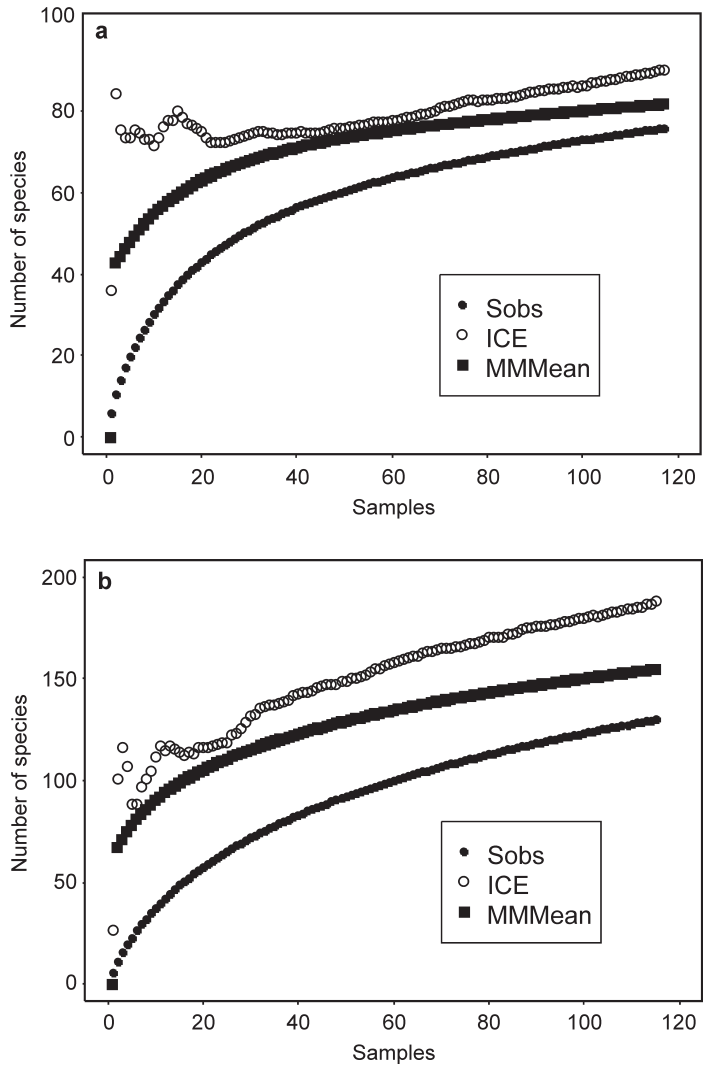

Fig. 2. Sample-based rarefaction curves indicating observed number of species (S_{obs} Mao Tao), incidence-based coverage estimator (ICE) and Michaelis-Menten mean (MMMean) richness estimators, of beetles (**a**) and spiders (**b**). In total, 120 samples were obtained for beetles and spiders (four treatments × five replicates per treatment × six sampling occasions = 120 samples).

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).

Beetle assemblages differed significantly across the four treatments (Global $R = 0.19$, $P = 0.005$). In the NMDS plot for beetles (Fig. 4), the replicates representing medium (M), high (H) and surrounded (S) treatments are clustered closely together on the left of the plot, indicating small assemblage differences among these treatments. Four of the control replicates (C1, C2, C4 & C5) form a second cluster on the right hand side of the plot, indicating that the assemblages of these replicates differ from those of the first cluster. C3 is on the edge of the first cluster and separate from the high and medium replicates. Considering those individual pairwise comparisons that were significant, the largest assemblage differences for beetles were between control *vs* surrounded treatments ($R = 0.43$), followed by high *vs* control treatments ($R = 0.35$) and medium *vs* control treatments ($R = 0.27$ – Table 2). As we did not find significant differences in assemblages, species richness or density between

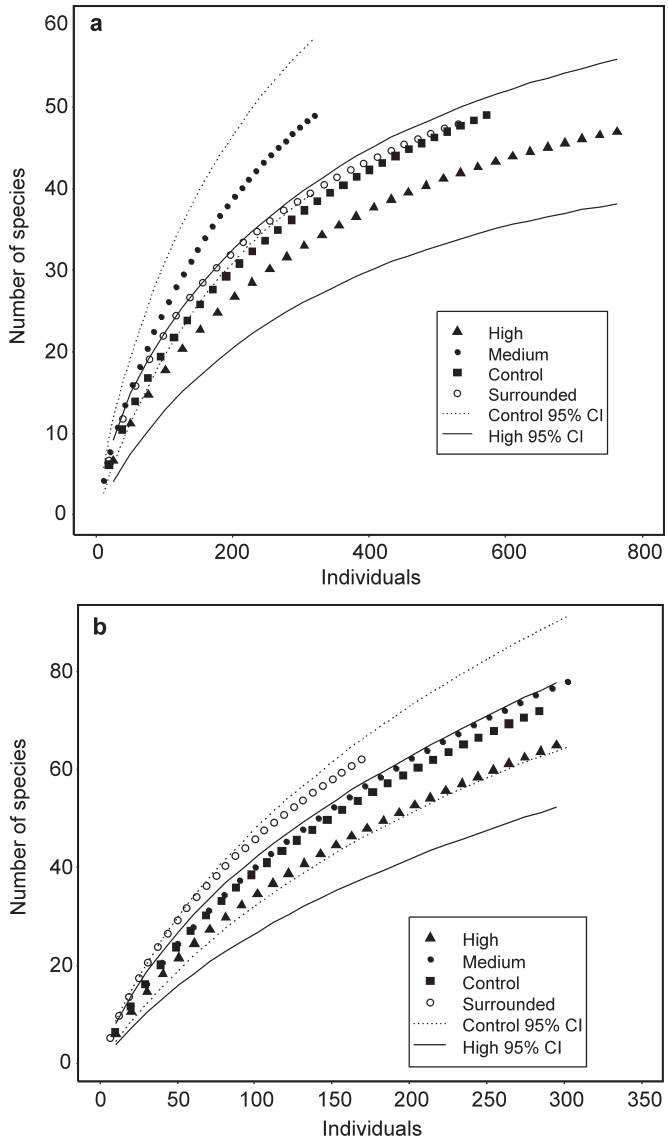

Fig. 3. Sample-based rarefaction curves (scaled by individuals) indicating observed number of beetle species (**a**) and spider species (**b**) (S_{obs}). Species richness should be compared when the number of individuals is equal in all treatments (i.e. approximately 340 individuals for beetles; approximately 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 $P > 0.05$.

medium and high treatments for either beetles or spiders, we pooled the data from the medium and high treatments into a single treatment called 'invaded' and repeated the ANOSIM analysis based on three treatments. The results of the ANOSIM comparing beetle assemblages across invaded, surrounded and control revealed a higher Global R statistic of 0.376 ($P = 0.001$) compared to the four treatments. The pairwise tests showed a significant difference between control and invaded ($R = 0.55$) and between control and surrounded ($R = 0.43$ – Table 2).

Overall, spider assemblages did not differ significantly across the four treatments (Global $R = 0.13$, $P = 0.06$). There is no clear separation of treatments in the NMDS plot for spiders (Fig. 5), which supports the low Global R statistic. However, the ANOSIM comparing spider assemblages across

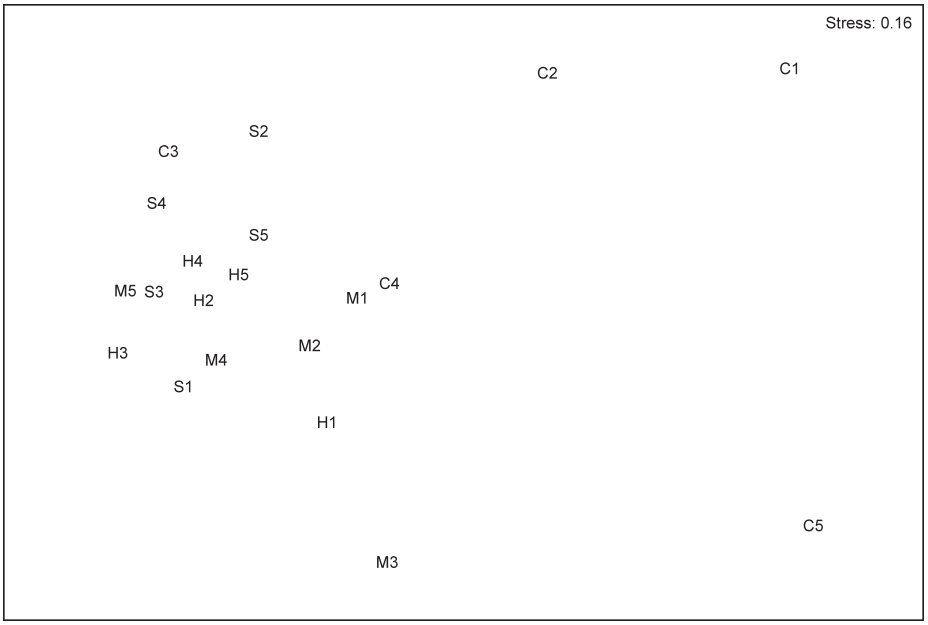

Fig. 4. Non-metric multidimensional scaling plot indicating similarity of beetle assemblages among replicates for four treatments. Treatments: H, high density; M, medium density; S, surrounded; C, control.

invaded, surrounded and control revealed a significant Global *R* statistic of 0.208 ($P = 0.027$). However, the only significant pairwise difference was between invaded and surrounded ($R = 0.257$, $P = 0.043$).

A total of 14 beetle species were unique to the control. Only three of these species were represented by three or more individuals (*Acmaeotethya virgo,* four individuals; *Orthophagus bicavifrons,* five individuals; *Philoserica vittata,* eight individuals). Only three beetle species were unique to the medium treatment and none were represented by three or more individuals. No beetle species were unique to the surrounded or high treatments. A total of 14 beetle species were found in the control treatment that were not present in either the medium or high treatments.

Table 2. Pairwise comparisons of beetle assemblages between treatments using analysis of similarity. The first ANOSIM compared assemblages among high, medium, control, and surrounded treatments. The second ANOSIM compared assemblages among invaded (a combination of high and medium), control and surrounded treatments. The *R* statistic is a measure of the similarity of assemblages. If *R* is significantly different from zero, then there are significant differences between assemblages. Significant values ($P < 0.05$) are in boldface.

Comparison	*R* statistic	*P*-value
High *vs* control	0.348	**0.02**
Medium *vs* control	0.268	**0.04**
Control *vs* surrounded	0.428	**0.01**
Medium *vs* high	–0.1	0.79
Medium *vs* surrounded	0.148	0.16
High *vs* surrounded	0.12	0.14
Invaded *vs* control	0.553	**0.003**
Control *vs* surrounded	0.428	**0.008**
Invaded *vs* surrounded	0.171	0.114

A total of 19 spider species were unique to the control. Of these only two species were represented by three or more individuals, including: *Oxyopes* sp. 2 (11 individuals) and *Runcinia flavida* (three individuals). A total of 15 spider species were unique to the medium treatment, with only one species being represented by three or more individuals (*Xerophaeus* sp. 1, four individuals). No spider species were unique to the surrounded or high treatments. A total of 25 spider species were found in the control that were not present in either the medium or high (invaded) treatments.

No beetle or spider species fulfilled the criteria for indicator species (IndVal ≥ 70%) in any of the treatments (high, medium, surrounded and control). When the high and medium treatments were combined (invaded treatment) one beetle species fulfilled the criteria for indicator species (*Graphipterus fasciatus distinctus* Péringuey, 1899; IndVal =

Fig. 5. Non-metric multidimensional scaling plot indicating similarity of spider assemblages among replicates for four treatments. Treatments: H, high density; M, medium density; S, surrounded; C, control.

70%, $P = 0.003$) for the invaded treatment. The beetle species with the highest IndVal for the control was *Acmaeodera virgo* Boheman, 1860 (IndVal = 60%, $P = 0.014$) and the highest IndVal for the surrounded was *Gymnopleurus ignitus* Klug, 1855 (IndVal = 66%, $P = 0.017$). The spider species with the highest IndVal for the control was *Runcinia flavida* (Simon, 1881) (IndVal = 60%, $P = 0.014$). The spider species with the highest IndVal for the invaded was *Loxosceles spiniceps* Lawrence, 1952 (IndVal = 59%, $P = 0.027$) and for surrounded was *Cheiramiona krugerensis* Lotz, 2002 that only had an IndVal of 43% which was not significant ($P = 0.09$).

Vegetation

The mean cover of plants that were less than one metre in height differed significantly across treatments (ANOVA, $F_{3,156} = 19.03$, $n = 20$, $P < 0.001$) (Fig. 6a). A Tukey test revealed that the cover of the high and medium treatments did not differ significantly from the control, that the surrounded treatment was significantly lower than the control, high and medium treatments (Fig. 6a). When

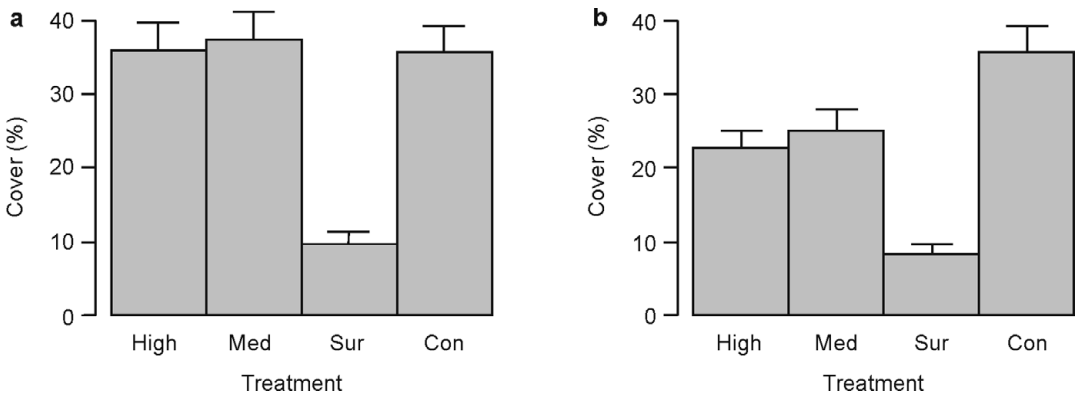

Fig. 6. Mean percentage vegetation cover (and standard error) measured in quadrats for each treatment, (**a**) for all species and (**b**) with *Opuntia stricta* excluded. Only plant species of less than 1 m in height were included. Treatments: High, high infestation; Med, medium infestation; Sur, surrounded; Con, control.

O. stricta was excluded from the dataset, the mean vegetation cover was much lower in the high and medium treatments, very slightly lower in the surrounded treatment and unaffected in the control (Fig. 6b). This shows the contribution of *O. stricta* to the vegetation cover in high and medium treatments was larger (13% reduction for high and 12% reduction medium) compared with the surrounded treatment (2% reduction). The percentage cover of *O. stricta* recorded in the quadrats differed significantly across treatments (ANOVA, $F_{3,156} = 16.86$, $n = 20$, $P < 0.001$). There was no significant difference in cover of *O. stricta* between high and medium treatments, but the high and medium treatments had significantly higher cover of *O. stricta* than control and surrounded treatments (Tukey test). The number of *O. stricta* plants along 10 m transects radiating out from the centre of each replicate was marginally non-significant among treatments (ANOVA, $F_{2,12} = 3.77$, $n = 15$, $P = 0.054$).

Plant assemblages differed significantly across the treatments (Global $R = 0.36$, $P = 0.001$). Plant assemblages of the high treatment were significantly different from the control ($R = 0.46$, $P = 0.008$) and the surrounded treatment ($R = 0.29$, $P = 0.04$), but not significantly different from the medium treatment ($R = 0.26$, $P = 0.09$). Plant assemblages of the medium treatment were significantly different from both control ($R = 0.32$, $P = 0.008$) and surrounded treatments ($R = 0.53$, $P = 0.008$). The plant assemblages of the control and surrounded treatments were significantly different ($R = 0.46$, $P = 0.008$).

DISCUSSION

For spiders we found that there were no significant differences in assemblages across treatments. Although we found significant differences in assemblages between invaded (by pooling the data from high and medium treatments) and the surrounded, the differences between invaded and control were not significant. The results suggest that current densities of *O. stricta* are not having a major impact on spider assemblages, species richness and species density. In contrast, Mgobozi *et al.* (2008) found significant impacts of an invasive shrub (*Chromolaena odorata*) on spider assemblages, richness and diversity in a South African savanna. Bultman & DeWitt (2008) found that ground-dwelling spider assemblages were substantially altered in broadleaf forest that was invaded by a herb (*Vinca major*) compared to uninvaded forest.

For beetles, we found a significant difference in assemblages between the medium treatment and control, and between the high treatment and control. However, species richness and species density did not differ significantly across treatments. Several studies that have investigated the impacts of invasive plants on arthropod diversity across a variety of habitats; both in 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) have found significant impacts on diversity. In a study by Coetzee *et al.* (2007) comparing dung beetle assemblages between wattle (*Acacia dealbata*) invaded grassland and uninvaded grassland, they found major differences in assemblages.

We found significantly higher abundances of beetles in the high treatment than the control. This is difficult to explain and contrasts with other studies that have reported decreases in abundance of arthropods in invaded ecosystems (French & Major 2001; Standish 2004; Ernst & Cappuccino 2005; Gerber *et al.* 2008).

No beetle or spider species could be considered to be reliable indicators of high or medium treatments. Only one beetle species fulfilled the criteria for indicator species (*Graphipterus fasciatus distinctus*) for the invaded treatment. This species can be used as an indicator of *O. stricta* invasion and it is possible that increased abundance of this species could indicate increased impact of *O. stricta* on beetle diversity. In contrast, reduced abundance of this species could indicate a decline in *O. stricta* impact, but further research will be required to confirm this. This species could be useful for setting TPC targets but ideally several species should be used to define these targets.

The cover of vegetation below one metre in height did not differ significantly among the control, high and medium treatments but was significantly lower in the surrounded treatment. The cover of *O. stricta* was significantly higher in the medium and high treatments than in the control and surrounded treatment. This confirms that *O. stricta* density is likely to explain the beetle assemblage differences between the medium treatment and control and between the high treatment and control. In comparing the assemblages between the control and the surrounded treatment, we wanted to determine whether the effect of *O. stricta* was confined to dense patches of this plant. Although we found a significant difference

in beetle assemblages between the control and surrounded treatment, the vegetation cover was significantly lower in the surrounded treatment than the control. We are thus not able to say whether the effects of *O. stricta* on beetle assemblages are confined to patches due to the confounding effect of vegetation cover.

The contribution of *O. stricta* to overall vegetation cover (<1 m) was relatively low at 12% for the medium and 13% for the high treatment. There were also no extensive areas (several hectares) invaded by *O. stricta* at high densities. Bultman & DeWitt (2008) reported significant changes in spider assemblages in forest invaded by *Vinca major* compared to uninvaded forest. They described the area invaded by this plant as 'a dense mat on the forest floor' and said that it 'forms a dense blanket of groundcover in forests'. This suggests that it probably has a higher cover and more radically transforms invaded areas than that of *O. stricta.* This could explain why they found substantial impacts on spider assemblages whereas we did not. In addition, Mgobozi *et al.* (2008) cited the decrease of habitat heterogeneity in savanna in KwaZulu-Natal (South Africa) 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 radically alters native vegetation structure and diversity. Harris *et al.* (2003) reported that the extent to which vegetation structure is altered could influence the degree to which spider assemblages differ from one another.

Although we did not quantify vegetation structure, the overall structure of the vegetation has not been radically altered when the two extremes are compared, namely the high treatment and the control. The high treatment and the control both contain trees in the canopy, a shrub layer and an herbaceous layer. The highly invaded treatment can therefore still be described as savanna vegetation and has a similar overall vegetation cover for plants less than 1 m in height to the control. This is in contrast to, for example, the case reported by Coetzee *et al.* (2007) where an invasive tree (*Acacia dealbata*) has invaded grassland and completely transformed the vegetation structure from grassland to what is effectively a forest.

A change in vegetation structure resulting from alien plant invasion has been cited as one of the principal causes of changes in arthropod assemblages (Standish 2004; Coetzee *et al.* 2007). Greenwood *et al.* (2004) attributed lower abundance and diversity of terrestrial arthropods to the simpler habitat structure and lower plant diversity in invaded areas. This notion is supported by the study of French & Eardley (1997) that found minimal impacts in litter invertebrate assemblages in shrub land invaded by *Chrysanthemoides monilifera* (Asteraceae) compared with native heath land of similar structure (i.e. height, canopy and leaf litter cover).

Changes in spider diversity and assemblages are expected to reflect habitat changes and changes in the arthropod community on which spiders prey, as spiders only interact indirectly with alien plants (Mgobozi *et al.* 2008). These results suggest that the invasion of *O. stricta* has not altered the habitats or the arthropod community (spider food sources) to the extent that it has resulted in detectable changes in spider assemblages. However, the invasion has altered the habitat sufficiently to result in assemblage differences for beetles. This suggests that beetles may be more sensitive to invasion of *O. stricta* than spiders. It has been suggested that food specialist herbivores are likely to be vulnerable to invasion (Tallamy 2004; Yoshioka *et al.* 2010). We expect that a proportion of the beetle species would be food specialist herbivores (whereas spiders are predators) and that beetles would be more directly dependent on plant composition than spiders.

It appears that at current densities *O. stricta* does not have a major impact on spider assemblages and diversity, although it does have an impact on beetle assemblages. We suggest that higher densities of *O. stricta,* resulting in greater habitat transformation, could have a greater impact on beetles and spiders and management should aim to prevent densities from increasing. Indeed, the *O. stricta* invasion in the KNP has shown a steady decrease in the size of the patches and the number of cladodes per plant. For example, Lotter (1996) reported 68 dense, impenetrable clumps of *O. stricta* and Hoffmann *et al.* (1998b) found several plants with more than 150 cladodes. In this study, we found only a few dense stands of *O. stricta* (approximately 15) and no plants with more than 150 cladodes. The decline in the density of *O. stricta* can be attributed to the biological control programme that was initiated in 1988. The management of *O. stricta* has been successful at reducing the density of this species to feasible maintenance levels. 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.* Given that beetle assemblages differ significantly between the invaded treatments (medium and high) and the control suggests that the density of *O. stricta* should be further reduced if possible.

CONCLUSION

At current densities, *Opuntia stricta* does not have a significant impact on spider assemblages, but beetle assemblages are affected. Beetle and spider species richness and species density were not significantly affected. The most likely explanation for these findings is that the current level of *O. stricta* invasion, maintained by the use of biological control, is insufficient to transform the structure of the vegetation to the extent that it significantly alters spider assemblages but that it is sufficient to alter beetle assemblages.

ACKNOWLEDGEMENTS

We thank the DST-NRF Centre for Invasion Biology and the University of Pretoria for financial support, Thomas Rikombe, Velli Ndlovu and Samson Ndlovu for their assistance in the field, James Harrison from the Ditsong National Museum of Natural History for assistance with the beetle identifications, and three anonymous reviewers whose comments helped to improve the manuscript.

REFERENCES

ANDERSEN, A.N. & MAJER, J.D. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* **2**: 291–298.

BULTMAN, T.L. & DEWITT, D.J. 2008. Effect of an invasive ground cover plant on the abundance and diversity of a forest floor spider assemblage. *Biological Invasions* **10**: 749–756.

CARRUTHERS, J. 1995. The Kruger National Park: a social and political history. University of Natal Press, Pietermaritzburg, South Africa.

CRAWLEY, M.J. 2007. *The R Book.* John Wiley & Sons, Chichester, England.

CHAZDON, R.L., COLWELL, R.K., DENSLOW, J.S. & GUARIGUATA, M.R. 1998. Statistical methods for estimating species richness of woody regeneration of primary and secondary rain forests of northeastern Costa Rica. In: *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies,* (eds) F. Dallmeier & J.A.Comiskey, pp. 285–309. Parthenon Publishing, Paris.

CHURCHILL, T.B. 1997. Spiders as ecological indicators: an overview for Australia. *Memoirs of the Museum of Victoria* **56**: 331–337.

CLARKE, K.R. & WARWICK, R.M. 2001. *Change In marine Communities: An Approach to Statistical Analysis and Interpretation,* 2nd edn. PRIMER-E, Plymouth.

CODDINGTON, J.A., YOUNG, L.H. & COYLE, F.A. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest. *Journal of Arachnology* **24**: 111–128.

COETZEE, B.W.T, VAN RENSBURG, B.J. & ROBERTSON, M.P. 2007. Invasion of grassland by silver wattle, *Acacia dealbata* (Mimosaceae), alters beetle (Coleoptera) assemblage structures. *African Entomology* **15**: 328–339.

COLWELL, R.K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application online at http://purl.oclc.org/estimates

COLWELL, R.K. & CODDINGTON, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* **345**: 101–118.

COLWELL, R.K., MAO, C.X. & CHANG, J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**: 2717–2727.

DUFRÊNE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**: 345–366.

ERNST, C.M. & CAPPUCCINO, N. 2005. The effect of an invasive vine, *Vincetoxicum rossicum* (Asclepiadaceae), on arthropod populations in Ontario old fields. *Biological Invasions* **7**: 417–425.

FOORD, S.H., MAFADZA, M.M., DIPPENAAR-SCHOEMAN, A.H. & VAN RENSBURG, B.J. 2008. Micro-scale heterogeneity of spiders (Arachnida: Araneae) in the Soutpansberg, South Africa: a comparative survey and inventory in representative habitats. *African Zoology* **43**: 156–174.

FOXCROFT, L.C. 2009. Developing thresholds of potential concern for invasive alien species: hypotheses and concepts. *Koedoe* **51**: 1–6.

FOXCROFT, L.C. & HOFFMANN, J.H. 2000. Dispersal of *Dactylopius opuntiae* (Cockerell) (Homoptera: Dactylopiidae), a biological control agent of *Opuntia stricta* (Haworth.) Haworth. (Cactaceae) in the Kruger National Park. *Koedoe* **43**: 1–5.

FOXCROFT, L.C. & RICHARDSON, D.M. 2003. Managing alien plant invasions in the Kruger National Park, South Africa. In: *Plant Invasions: Ecological Threats and Management Solutions,* (eds) L.E. Child, J.H., Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade & M. Williamson, pp. 385–403. Backhuys Publishers, Leiden.

FOXCROFT, L.C., HOFFMANN, J.H., VILJOEN, J.J. & KOTZE, J.J. 2007. Factors influencing the distribution of *Cactoblastis cactorum,* a biological control agent of *Opuntia stricta* in Kruger National Park, South Africa. *South African Journal of Botany* **73**: 113–117.

FOXCROFT, L.C. & DOWNEY, P.O. 2008. Protecting biodiversity by managing alien plants in national parks: perspectives from South Africa and Australia. In: *Plant Invasions: Human Perception, Ecological Impacts and Management,* (eds) B. Tokarska-Guzik, J.H. Brock, G. Brundu, L. Child, C.C. Daehler & P. Pyssek, pp. 387–403. Backhuys Publishers, Leiden.

FRENCH, K. & EARDLEY, K. 1997. The impact on weed infestations on litter invertebrates in coastal vegeta-

tion. In: *Frontiers in Ecology: Building the Links,* (eds) N. Klomp & I. Lunt, I., pp. 89–102. Elsevier Science, Oxford.

FRENCH, K. & MAJOR, R.E. 2001. Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Austral Ecology* **26**: 303–310.

FRIDLEY, J.D., STACHOWICZ, J.J., NAEEM, S., SAX, D.F., SEABLOOM, E.W., SMITH, M.D., STOHLGREN, T.J., TILMAN, D. & VON HOLLE, B. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88**: 3–17.

GERBER, E., KREBS, C., MURRELL, C., MORETTI, M., ROCKLIN, R. & SCHAFFNER, U. 2008. Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation* **141**: 646–654.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**: 9–121.

GOTELLI, N.J. & COLWELL, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379–391.

GRATTON, C. & DENNO, R.F. 2005. Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restoration Ecology* **13**: 358–372.

GREENWOOD, H., O'DOWD, D.J. & LAKE, P.S. 2004. Willow (*Salix* × *rubens*) invasion of the riparian zone in south-eastern Australia: reduced abundance and altered composition of terrestrial arthropods. *Diversity and Distributions* **10**: 485–492.

HARRIS, K.R. 2009. Arthropod assemblages in a savanna invaded by *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. M.Sc. thesis, University of Pretoria, Pretoria.

HARRIS, R., YORK, A. & BEATTIE, A.J. 2003. Impacts of grazing and burning on spiders assemblages in dry eucalypt forests of north-eastern New South Wales, Australia. *Austral Ecology* **28**: 526–538.

HOFFMANN, J.H., MORAN, V.C. & ZELLER, D.A. 1998a. Evaluation of *Cactoblastis cactorum* (Lepidoptera: Phycitidae) as a biological control agent of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Biological Control* **12**: 20–24.

HOFFMANN, J.H., MORAN, V.C. & ZELLER, D.A. 1998b. Long-term population studies and the development of an integrated management programme for control of *Opuntia stricta* in Kruger National Park, South Africa. *Journal of Applied Ecology* **35**: 156–160.

KENNEDY, T.A., NAEEM, S., HOWE, K.M., KNOPS, J.M.H., TILMAN, D. & REICH, P. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**: 636–638.

LONGINO, J.T., CODDINGTON, J.A. & COLWELL, R.K. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* **83**: 689–702.

LONSDALE, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**: 1522–1536.

LOTTER, W.D. 1996. Strategic management plan for the control of *Opuntia stricta* in the Kruger National Park. Scientific report 17/96. National Parks Board, Skukuza, South Africa.

LOTTER, W.D. & HOFFMANN, J.H. 1998. An integrated management plan for the control of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Koedoe* **41**: 63–68.

MAGURRAN, A.E. 2004. *Measuring Biological Diversity.* Blackwell Science, Malden, U.K.

McGEOCH, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* **73**: 181–201.

McGEOCH, M.A., VAN RENSBURG, B.J. & BOTES, A. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology* **39**: 661–672.

MGOBOZI, P.M., SOMERS, M.J. & DIPPENAAR-SCHOEMAN, A.S. 2008. Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *Journal of Applied Ecology* **45**: 1189–1197.

NOSS, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**: 355–364.

PEARCE, J.L. & VENIER, L.A. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecological Indicators* **6**: 780–793.

PÉTILLON, J., YSNEL, F., CANARD, A. & LEFEUVRE, J. 2005. Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. *Biological Conservation* **126**: 103–117.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for statistical Computing, Vienna, Austria. Online at: http://www.R-project.org

RAINIO, J. & NIEMELÄ, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* **14**: 487–506.

SAMWAYS, M.J. & MOORE, S.D. 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation* **57**: 117–137.

SAMWAYS, M.J., CALDWELL, P.M. & OSBORN, R. 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment* **59**: 19–32.

SAMWAYS, M.J. & TAYLOR, S. 2004. Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata). *South African Journal of Science* **100**: 78–79.

SCHOLES, R.J. 1997. Savanna. In: *Vegetation of Southern Africa,* (eds) R.M. Cowling, D.M. Richardson & S.M. Pierce. Cambridge University Press, Cambridge.

SCOTT, A.G., OXFORD, G.S. & SELDEN, P.A. 2006. Epigaeic spiders as ecological indicators of conservation value for peat bogs. *Biological Conservation* **127**: 420–428.

STANDISH, R.J. 2004. Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand. *Biological Conservation* **116**: 49–58.

STEENKAMP, H.E. & CHOWN, S.L. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: Scarabaeinae) assemblage in southern Africa. *Biological Conservation* **78**: 305–311.

STOHLGREN, T.J., BARNETT, D. & KARTESZ, J. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* **1**: 11–14.

TALLAMY, D.W. 2004. Do alien plants reduce insect biomass? *Conservation Biology* **18**:1689–1692.

TOFT, R.J., HARRIS, R.J. & WILLIAMS, P.A. 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biological Conservation* **102**: 31–46.

TOTI, S.D., COYLE, F.A. & MILLER, J.A. 2000. A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. *Journal of Arachnology* **28**: 329–345.

USHER, M.B. 1988. Biological invasions of nature reserves: a search for generalization. *Biological Conservation* **44**: 119–135.

VAN RENSBURG, B.J., McGEOCH, M.A., CHOWN, S.L. & VAN JAARSVELD, A.S. 1999. Conservation of heterogeneity among dung beetles in the Maputaland Centre of Endemism, South Africa. *Biological Conservation* **88**: 145–153.

VAN WILGEN, B.W. 2004. Scientific challenges in the field of invasive alien plant management. *South African Journal of Science* **100**: 19–20.

VOLCHANSKY, C.R., HOFFMANN, J.H. & ZIMMERMANN, H.G. 1999. Host-plant affinities of two biotypes of *Dactylopius opuntiae* (Homoptera: Dactylopiidae): enhanced prospects for biological control of *Opuntia stricta* (Cactaceae) in South Africa. *Journal of Applied Ecology* **36**: 85–91.

WILSON, E.O. 1987. The little things that run the world (The importance and conservation of invertebrates). *Conservation Biology* **1**: 344–346.

YOSHIOKA, A., KADOYA, T. SUDA, S. & WASHITANI, I. 2010. Impacts of weeping lovegrass (*Eragrostis curvula*) invasion on native grasshoppers: responses of habitat generalist and specialist species. *Biological Invasions* **12**: 531–539.

Responsible Editor: J.H. van Wyk

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

Species	High infestation	Medium infestation	Surrounded	Control
ORDER COLEOPTERA				
Buprestidae				
Acmaeodera luteopicta Fåhraeus, 1851				1
Acmaeodera virgo Boheman, 1860				4
Carabidae				
Abacetus auspilatus Péringuey				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 Péringuey, 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 Gerstëcker, 1855				1

Species	High infestation	Medium infestation	Surrounded	Control
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. i*ctericus*	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

Species	High infestation	Medium infestation	Surrounded	Control
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				
Agelenidae				
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 (Forsskål, 1775)	4	3	1	1
Hypsosinga lithyphantoides Caporiacco, 1947*	1	1		1
Isoxya stuhlmanni (Bösenberg & Lentz, 1885)	2	1		
Neoscona blondeli (Simon, 1885)	2	1	1	
Pararaneus cyrtoscapus (Pocock, 1898)*			1	
Prasonica albolimbata Simon, 1895				
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		
Merenius alberti Lessert, 1923	2	1	2	
Messapus martini Simon, 1898*	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				
Paradonea 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		

Species	High infestation	Medium infestation	Surrounded	Control
Asemesthes sp. 1*	12	10	7	22
Drassodes masculus Tucker, 1923*	4	1	1	
Drassodes splendens Tucker, 1923*		1	5	4
Drassodes stationis Tucker, 1923*			1	
Pterotricha auris (Tucker, 1923)	4	6	2	4
Ibaba arcus (Tucker, 1923)	3	4		13
Setaphis browni (Tucker, 1923)		1		
Xerophaeus bicavus Tucker, 1923		4		
Zelotes corrugata (Purcell, 1907)		2	2	3
Zelotes natalensis Tucker, 1923*		1		
Zelotes scrutatus (O.P. Cambridge 1872)*			1	
Zelotes tuckeri Roewer 1951*	3	4	7	1
Zelotes sp. 1		1		
Idiopidae				
Segregara mossambicus (Hewitt, 1919)*		1		
Lycosidae				
Arctosa transvaalana Roewer, 1960				1
Geolycosa natalensis Roewer, 1960	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 guttata (Karsch, 1876)				1
Pardosa crassipalpis Purcell, 1903*	2	3	4	9
Pardosa sp. 2*	5	1	5	4
Trabea purcelli Roewer, 1951				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 schenkeli Lessert, 1927	1	1	1	2
Oxyopes sp. 2				1
Peucetia viridis (Blackwall, 1858)	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	

Species	High infestation	Medium infestation	Surrounded	Control
Euprosthenopsis pulchella (Pocock, 1902)*	1	2	1	1
Maypacius bilineatus (Pavesi, 1895)*		1		1
Prodidomidae				
Austrodomus zuluensis Lawrence, 1947*	1			
Salticidae				
Aelurillus sp. 1		1		
Baryphas ahenus Simon, 1902	2		2	3
Evarcha dotata (Peckham & Peckham, 1903)	2	1		3
Hyllus argyrotoxus Simon, 1902*	13	5	9	5
Hyllus treleaveni Peckham & Peckham, 1902*	2	3	1	
Langelurillus sp. 1*	2	1		
Langona manicata Simon, 1901*			1	
Mexcala rufa Peckham & Peckham, 1902 sp. 1*		1		1
Natta chionogastra (Simon, 1901)*		8	4	
Stenaelurillus guttiger (Simon, 1901)*	5	1		4
Stenaelurillus nigricaudus Simon, 1885*	2		1	7
Stenaelurillus sp. 3*		2		2
Stenaelurillus sp. 4*	4	3	1	2
Thyene coccineovittata (Simon, 1885)	1	1		3
Thyenula aurantiaca (Simon, 1902)*	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 zuluana Lawrence, 1937*	2			
Panaretella sp. 1		1		2
Tetragnathidae				
Leucauge festiva (Blackwall, 1866)	2			
Theraphosidae				
Augacephalus breyeri (Hewitt, 1919)			1	2
Ceratogyrus darlingi Pocock, 1897	1			
Ceratogyrus dolichocephalus Hewitt 1919	1			
Idiothele nigrofulva (Pocock, 1898)		1	2	
Pterinochilus lugardi Pocock, 1900*	1	6	4	3
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

Species	High infestation	Medium infestation	Surrounded	Control
Simorcus cotti Lessert, 1936	1			
Stiphropus bisigillatus Lawrence, 1952*				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			