

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

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Summary

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

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

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

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

5. *Synthesis and applications.* Alien clearance is an essential and invaluable management tool. There are a substantial number of programmes that aim to control alien invasive plants but very little is known about the way in which biodiversity recovers after alien plant removal. Our data show that the removal of alien invasive plants benefits biodiversity with immediate effects, highlighting that management should be carried out to control this invasive, even if the area has been invaded for a long period of time. These data are important for policy-forming and informing policy-makers that alien invasion and removal are critical for biodiversity conservation management.

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

Introduction

South Africa is one of the countries most seriously affected by alien plant invasions (Richardson & van Wilgen 2004). Invasive weeds alter vegetation structure in the areas they invade, leading to lower native plant species richness (Knops *et al.* 1999). Some invasive species may also be considered to be ecological engineers as they modify the ground surface micro-environment in encroached areas (Pétillon *et al.* 2005).

Invasions by alien plants into unspoiled ecosystems are a cause for high concern because the pristine systems are important stores of biodiversity (Higgins *et al.* 1999). Indeed, the introduction of non-indigenous species into protected areas is a direct threat to conservation (Blossey 1996). Consequently, it is fundamental to document the impact that alien invasive plants have on native communities and to determine if, and at what rate, native communities re-establish following the removal of invasives (Gratton & Denno 2005). A thorough understanding of an invasion is necessary for the development of basic ecological principles used for its management

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(D'Antonio & Vitousek 1992). Since the effect of invasive species can be slow and cumulative, extending over time, most studies on the effects of invasive species lack a temporal context (Strayer *et al.* 2006).

Trifid weed *Chromolaena odorata* (L.) R.M. King and H. Robinson (Asteraceae) is native to South and Central America. It grows rapidly and forms impenetrable tangles that may ultimately shade out all the indigenous vegetation (Macdonald 1983). Through physical smothering and allelopathy, *C. odorata* reduces vegetation heterogeneity in grasslands, savannas and forests (Goodall & Zachariades 2002). *Chromolaena odorata* has naturalized in many parts of the world (Ambika & Jayachandra 1990) and has been noted as one of the most important invader species in the savanna biome in South Africa (Richardson & van Wilgen 2004). Robertson *et al.* (2003) ranked *C. odorata* as the second worst alien weed species to cause problems in South Africa after lantana *Lantana camara* L. Accordingly, *C. odorata* has become a major problem in conservation areas and is the most widespread invader posing the greatest threat to the natural vegetation in Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal in South Africa (Macdonald 1983; Howison & Balfour 2002). *Chromolaena odorata* was first recorded in HiP in 1961. In 1983, the distribution of *C. odorata* was mapped for the first time, revealing 50 ha of infestation (Macdonald 1983). Re-mapping in 1998 showed 2100 ha of infestation (Howison & Balfour 2002).

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

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

Materials and methods

STUDY AREA

Data were collected from Hluhluwe-iMfolozi Park, which lies between the latitudes 28°00' and 28°26' S and longitudes 31°43' and 32°09' E. HiP is located in the foothills of the escarpment to the west of the coastal plain in central KwaZulu-Natal, South Africa. It encompasses 900 km² and is comprised of a northern section, Hluhluwe (300 km²) and a southern section, iMfolozi and corridor (600 km²). This Park has unimodal rainfall (Macdonald 1983); the mean annual rainfall is 990 mm in Hluhluwe and 720 mm in iMfolozi (Wateley & Porter 1983). The Park's environment and vegetation are described by Wateley & Porter (1983).

EXPERIMENTAL DESIGN AND SAMPLING METHODS

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

Pitfall traps

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

Vegetation beating

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

DATA ANALYSES

The data from the two sampling methods were analysed separately as they are designed to target different assemblages and because no vegetation (*C. odorata*) beating was done in the control sites. Species accumulation curves for the two sampling methods were used to determine sampling adequacy. Because the data could not be transformed to be normally distributed, non-parametric tests Mann–Whitney U (U) and Kruskal–Wallis analysis of variance (H) (ANOVA) were applied to the data with the software program STATISTICA version 6 (<http://www.statsoft.com>). Non-parametric species richness estimators were computed using the ESTIMATES version 7 software program (<http://viceroy.eeb.uconn.edu/estimates>). To examine differences in spider assemblages between the different sites, the following diversity indices were calculated using the PRIMER version 5 software (Plymouth Routines in Multivariate Ecological Research) (Clarke & Warwick 2001): total number of specimens (N), alpha diversity (S), Shannon–Wiener (H'), Simpson's ($1 - \lambda$) and Margalef's (d) (Clarke & Warwick 2001).

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

were used to determine which species contributed to the observed patterns of species distributions in the different sites. Geometric class plots were used to determine differences in species classes between the cleared sites, where species abundance distributions were assessed. Geometric class plots are frequency polygons for a pooled set of samples and number of species fall into a set of geometric abundance classes. These were plotted by the number of classes represented in the sample (i.e. one individual, class 1; two to three individuals, class 2; four to seven individuals, class 3, etc.). Since spiders live in defined environments and have limitations set by physical conditions and biological factors (Foelix 1982), their species can be grouped into guilds based on the available information on their preferred habitats and predatory strategies (Dippenaar-Schoeman *et al.* 2005). Therefore, the spiders were allocated to their guilds primarily using Dippenaar-Schoeman *et al.* (2005) and secondarily Dippenaar-Schoeman & Jocquè (1997). The guilds they were allocated can be divided into two main groups; namely, web builders (WB) and wanderers (W). The web builders construct the following types of webs: funnel web (FWB), orb web (OWB), sheet web (SWB), gumfoot web (GFWB). The free-living wanderers were defined as: free-living ground-dweller (GD), burrowing ground-dweller (BGD) and plant-dweller (PD) (Supplementary Material Appendix S1).

Results

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

DO *C. ODORATA* INVASIONS ALTER SPIDER ASSEMBLAGE PATTERNS?

The control sites had the highest abundance, alpha diversity, Margalef's diversity and Shannon–Wiener diversity for pitfall trap data in comparison to sites invaded with *C. odorata* for different invasion durations and to cleared sites (Table 1). These results proved not to be significant; however Fig. 1a demonstrated the trend that the control sites had higher species richness than invaded sites. Of interest was that both sites that have been invaded for the longest duration had similarly lower species richness (Fig. 1a).

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

Diversity index	Control	< 2 years		10 years		20 years		Cleared 2 years		Cleared 5 years	
	PT	PT	VB	PT	VB	PT	VB	PT	VB	PT	VB
N	240.0	230.0	190.0	200.0	80.0	70.0	173.0	180.0	290.0	170.0	190.0
S	112.5	102.5	125.0	70.0	60.0	57.5	115.0	84.7	130.0	84.4	113.0
d	32.6	30.0	40.1	21.6	20.4	23.0	36.9	26.9	35.5	27.0	35.0
$H'(\log_e)$	19.2	17.9	24.0	14.9	13.6	15.9	22.7	17.1	22.5	17.2	21.6
$1 - \lambda$	08.0	07.5	09.4	07.5	06.3	08.9	09.3	08.1	09.0	08.1	09.0

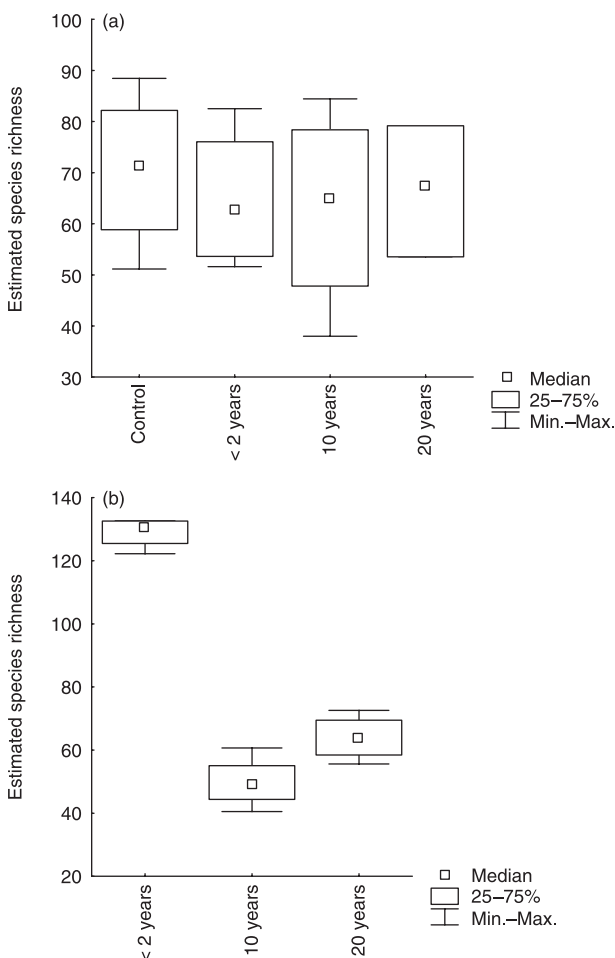


Fig. 1. Estimated species richness with invasion duration for (a) pitfall trap data ($H_{3,15} = 01.75$, $P > 00.5$) and (b) vegetation beating data ($H_{2,12} = 92.69$, $P < 00.1$).

DO DIFFERENT INVASION DURATIONS OF *C. ODORATA* HAVE A VARYING EFFECT ON NATIVE SPIDER ASSEMBLAGE PATTERNS?

As anticipated, with increasing invasion duration, the pitfall trap data showed (from new invasion to 20-year invasion) an overall declining trend in abundance and alpha diversity of spiders caught (Table 1). As vegetation beating was designed

to observe if there were any spider species that inhabited this invasive weed, the 10-year invasion sites had the highest abundance, with the newly invaded sites (< 2 years) having the lowest abundance (Table 1). Interestingly, similar to pitfall trap data, the vegetation beating data showed the higher diversity to be in the newly invaded sites and the lowest in the sites that have been invaded for longer durations (Table 1).

The observed differences from the diversity indices in Table 1 were not significant. However, non-parametric species richness estimators (jackknife second order) further showed a similar trend of richness declining with invasion duration for pitfall trap data (Fig. 1a), and vegetation beating data further proved these trends to be significant ($H_{2,12} = 9.269$, $P < 00.1$) (Fig. 1b). The site that had been invaded for 20 years had the highest overall contribution of Zodariidae which is a specialist in disturbed habitats, and the 10 years invaded site had the highest overall contribution of Salticidae which is a generalist tolerant of dry habitat (see Supplementary Material Appendix S1). The MDS ordination revealed significant differences in spider assemblage patterns due to different invasion durations (Fig. 2) ($R = 04.42$, $P < 00.1$). Moreover, there were no significant differences between the sites that were invaded for longer durations amongst themselves; however, significant differences were observed when comparing the sites that have been invaded for longer durations to sites that have been newly invaded (Fig. 2). SIMPER routine further revealed that the newly invaded sites (< 2 years) had the highest number of spider species uniquely characteristic to these sites (Table 2), and no significant differences in spider guild structures were observed when comparing sites of different invasion durations.

DO NATIVE SPIDER ASSEMBLAGES RE-ESTABLISH AFTER *C. ODORATA* CLEARANCE WITHOUT FURTHER MANAGEMENT INTERVENTION?

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

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

	Av. abund		Av. sim		Contrib%	
	PT	VB	PT	VB	PT	VB
Control						
<i>Anahita sp 1</i> ■	12.5	n/a	21.1	n/a	73.5	n/a
<i>Cydrela sp 1</i> ■	17.5	n/a	26.3	n/a	91.5	n/a
<i>Hogna sp 1</i> ▲	57.5	n/a	94.0	n/a	326.7	n/a
<i>Pardosa sp 1</i> ▲	62.5	n/a	117.6	n/a	408.8	n/a
< 2 years						
<i>Araneilla sp 1</i>	–	05.0	–	11.1	–	36.4
<i>Asemesthes ceresicola</i> •	07.5	–	22.3	–	86.8	–
<i>Cheiracanthium vansoni</i>	–	17.5	–	63.4	–	207.8
<i>Clubiona sp 1</i>	–	10.0	–	33.4	–	109.5
<i>Cyphalonotus larvatus</i> °	–	05.0	–	10.4	–	34.0
<i>Heliophanus sp 1</i> °	–	05.0	–	11.9	–	39.0
<i>Lycosa sp 1</i> •	07.5	–	24.2	–	94.5	–
<i>Olios sp 2</i> •	–	05.0	–	10.4	–	34.1
<i>Pardosa sp 1</i> ▲	62.5	–	76.4	–	297.8	–
<i>Stenaehurillus sp 1</i> •	10.0	–	22.3	–	86.8	–
<i>Thyene inflata</i>	–	25.0	–	123.1	–	403.0
<i>Tmarus cameliformis</i>	–	05.0	–	11.9	–	39.0
10 years						
<i>Olios correvoni</i>	–	20.0	–	29.6	–	71.8
<i>Pardosa sp 1</i> ▲	22.5	–	104.1	–	341.1	–
<i>Setaphis sp 1</i>	–	10.0	–	17.5	–	42.4
<i>Thyene inflata</i>	–	72.5	–	198.4	–	481.3
<i>Thomisops pupa</i>	–	22.5	–	35.0	–	84.9
<i>Tmarus cameliformis</i>	–	12.5	–	13.9	–	33.7
20 years						
<i>Araneilla sp 1</i>	–	05.0	–	11.5	–	63.2
<i>Caesetius sp 1</i> •	05.0	–	09.8	–	45.2	–
<i>Evarcha sp 1</i>	–	10.0	–	07.1	–	39.0
<i>Heriaeus buffoni</i> •	05.0	–	09.8	–	45.2	–
<i>Hogna sp 1</i> ▲	20.0	–	83.8	–	386.1	–
<i>Olios correvoni</i>	–	12.5	–	11.5	–	63.2
<i>Pardosa sp 1</i> ▲	27.5	–	27.4	–	126.5	–
<i>Synema nigrotibiale</i> °	–	05.0	–	07.2	–	39.8
<i>Thomisops pupa</i>	–	10.0	–	13.3	–	73.3
<i>Tmarus cameliformis</i>	–	22.5	–	38.3	–	210.7
<i>Zelotes tuckeri</i>	12.5	–	72.3	–	333.1	–
Cleared 2 years ago						
<i>Araneus sp 1</i> °	–	10.0	–	29.0	–	196.4
<i>Cheiracanthium vansoni</i>	–	10.0	–	29.0	–	196.4
<i>Clubiona sp 1</i>	–	10.0	–	60.6	–	410.7
<i>Hogna sp 1</i> ▲	42.5	–	68.2	–	265.2	–
<i>Pardosa sp 1</i> ▲	85.9	–	128.7	–	501.0	–
<i>Thyene inflata</i>	–	06.7	–	29.0	–	196.4
Cleared 5 years ago						
<i>Anahita sp 1</i> ■	15.0	–	21.9	–	85.1	–
<i>Araneilla sp 1</i>	–	10.0	–	08.3	–	29.7
<i>Cheiracanthium vansoni</i>	–	10.0	–	29.4	–	105.0
<i>Clubiona sp 1</i>	–	10.0	–	15.5	–	55.3
<i>Corinnidae sp 1</i> •	–	05.0	–	11.5	–	41.0
<i>Cydrela sp 1</i> ■	10.0	–	29.0	–	112.7	–
<i>Diaea puncta</i> •	–	10.0	–	08.3	–	29.7
<i>Evarcha sp 1</i>	–	10.0	–	26.8	–	95.7
<i>Hogna sp 1</i> ▲	42.5	–	68.2	–	265.2	–
<i>Olios correvoni</i>	–	07.5	–	26.8	–	95.7
<i>Pardosa sp 1</i> ▲	15.0	–	128.7	–	501.0	–
<i>Thomisops pupa</i>	–	12.5	–	34.4	–	122.7
<i>Thyene inflata</i>	–	30.0	–	88.0	–	314.2
<i>Thyene natalii</i> °	–	07.5	–	08.3	–	29.7
<i>Anahita sp 1</i>	07.5	–	38.8	–	127.0	–
<i>Evarcha sp 1</i>	–	25.0	–	50.4	–	122.3
<i>Hogna sp 1</i> ▲	50.0	–	152.6	–	499.7	–
<i>Anahita sp 1</i>	07.5	–	38.8	–	127.0	–

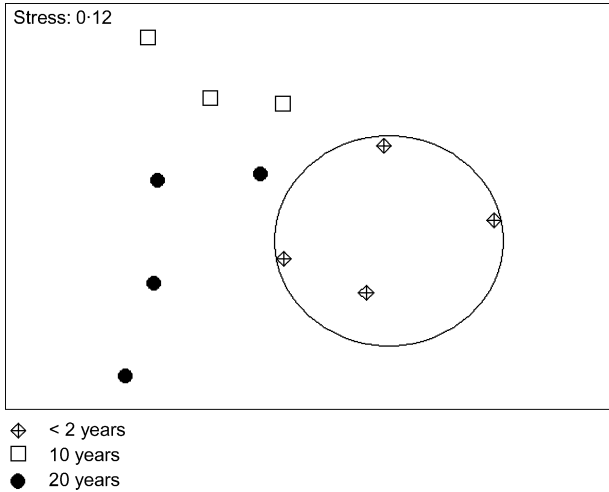


Fig. 2. Multidimensional scaling ordination based on Bray–Curtis similarity matrix derived from fourth root-transformed ground-dwelling spider data demonstrating different spider assemblages due to different invasion durations. The plot is significant ($R = 0.42$, $P < 0.01$), the pairwise tests revealed significant differences between the new invasion < 2 years and 10 years invasion ($R = 0.67$, $P = 0.029$) and no significant differences between 10 years invasion and 20 years invasion.

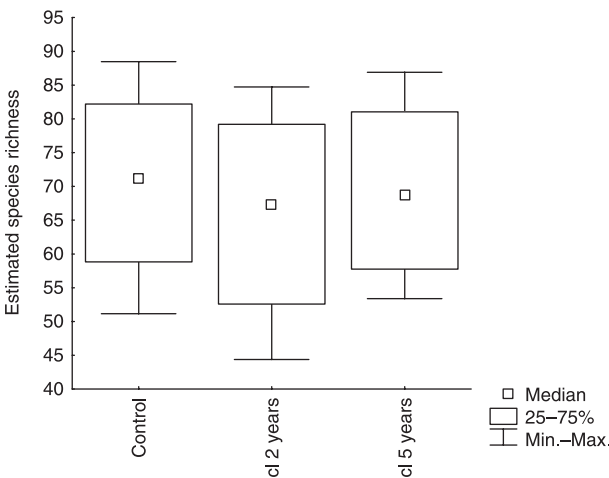


Fig. 3. Estimated species richness for the cleared sites for pitfall trap data ($H_{2,12} = 0.5000$, $P > 0.05$) illustrating non-significant differences to the estimated species richness of the control sites in comparison to the cleared sites. ‘cl’ denotes cleared.

(Fig. 4) as there were no significant differences ($R = -0.174$, $P > 0.05$) with the negative R value, denoting that these sites could be from the same sample. Also, no significant differences for guild structures were observed when comparing the cleared sites to the control sites. However, the results further show that, although the system is rehabilitating after *C. odorata* clearance, there are two families that occurred only in the control, namely Cyrtaucheniidae (trap door spider) and Uloboridae (lace orb-web spiders) (see Supplementary Material Appendix S1).

Of interest was the high estimated species richness (Fig. 5) and abundance (Fig. 6a) in re-established *C. odorata* sites that have been cleared for a longer duration (cleared 5 years ago) than recently cleared sites (cleared 2 years ago). Of more

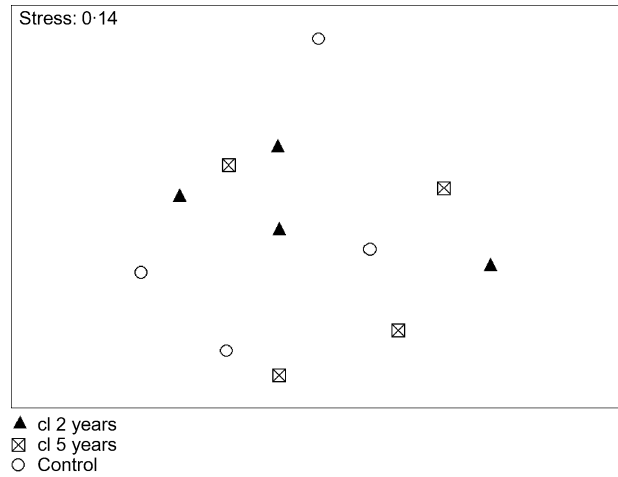


Fig. 4. Multidimensional scaling ordination based on fourth root-transformed ground-dwelling spider data demonstrating similarity in spider assemblages in the control and the cleared sites ($R = -0.174$, $P < 0.01$) where the negative value denotes that these sites could be from the sample population.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

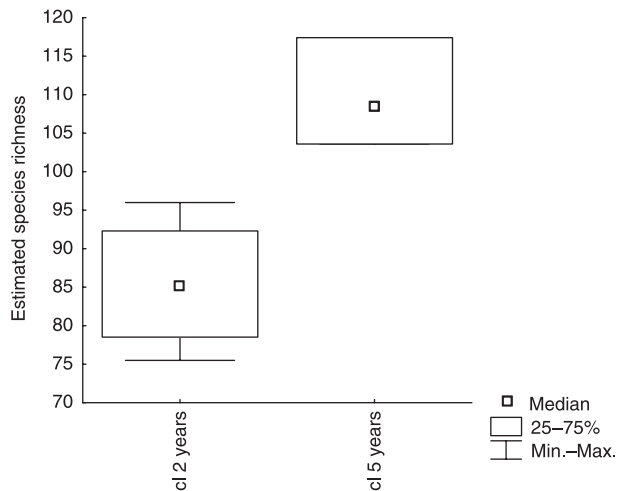


Fig. 5. Estimated species richness for the cleared sites for vegetation beating data ($U = 0.000$, $z = -2.1213$, $P < 0.05$). Illustrating a higher estimated species richness for spiders inhabiting the *C. odorata* plant in the sites cleared for 5 years in comparison to sites that have been cleared 2 years ago. ‘cl’ denotes cleared.

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

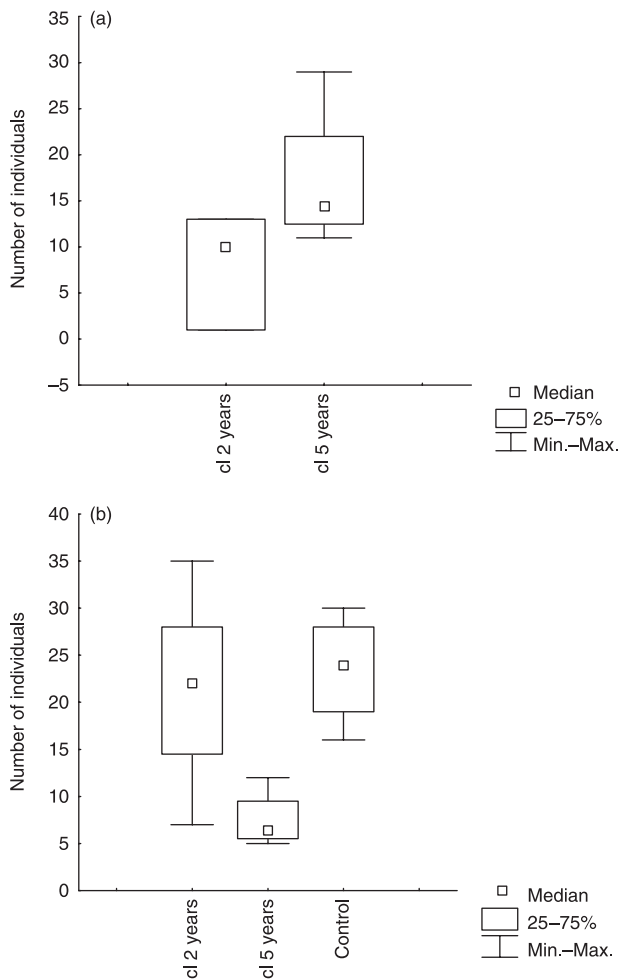


Fig. 6. Abundance of spiders in the cleared sites: (a) vegetation beating data showed that the spiders inhabiting *C. odorata* plants had the highest abundance in the site that was cleared 5 years ago and lowest in the site cleared 2 years ago ($U_{2,12} = 10.00$, $P > 0.05$) while the converse held true for pitfall trap data, (b) with the highest abundance in the control and the lowest in the site cleared 5 years ago ($H_{2,16} = 76.39$, $P < 0.05$). 'cl' denotes cleared.

Discussion

Chromolaena odorata invasions do alter native spider assemblage patterns. Lower diversity and species richness was observed in invaded sites in comparison to uninvaded sites. Additionally, progressive invasion of *C. odorata* brings with it changes in native spider abundance, diversity (Table 1), assemblage patterns (Fig. 2) and estimated spider species richness (Fig. 1a,b). The results show that *C. odorata* invasion alters and radically changes spider assemblages native to these habitats. Similarly, Greenwood *et al.* (2004) demonstrated distinct grouping between the native and the invaded sections, which indicated that the invasion had a strong overall effect on the species composition of terrestrial arthropods. The still relatively high species richness in newly invaded sites suggests that these sites have not been drastically altered or transformed by the invasion of *C. odorata*, and that there is still a high proportion of indigenous vegetation and thus a larger

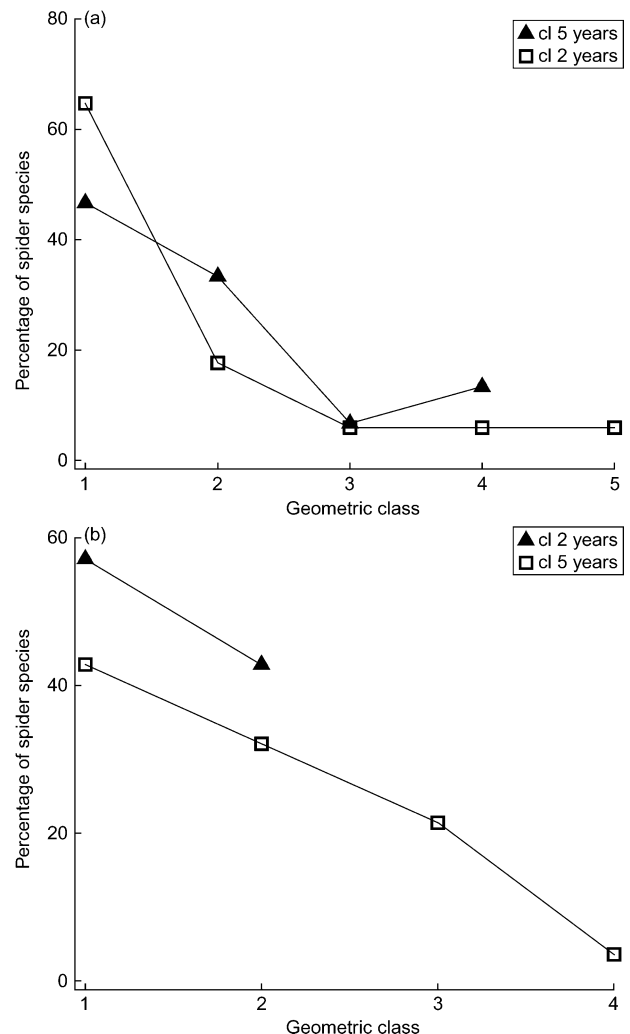


Fig. 7. The geometric class plot for the spider species illustrates a higher percentage contribution of rare species for the recently cleared sites (2 years) for both a) pitfall trap and b) vegetation beating data. However, pitfall trap data (a) illustrates that the site that has been recently cleared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

pool of spiders which invariably also inhabit the invasive plant. Harris, York & Beattie (2003) found that the extent to which native invertebrate communities are restructured may vary with the extent of change to the vegetation structure. As a result, a habitat may be able to accommodate a substantial number of alien plants before there is a negative impact on the insect consumers in that habitat (Tallamy 2004). The significantly higher species richness in newly invaded sites as opposed to the sites that have been invaded for longer durations demonstrates the negative impacts associated with cumulative invasion duration of *C. odorata* on spider communities (Fig. 1b). It has been found that the lower abundance and diversity of terrestrial arthropods in invaded sections than uninvaded sections is due to simpler habitat structure and lower plant diversity in invaded sections (Greenwood *et al.*

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

On the positive side, the effects of alien plant invasion on spider communities appear to be mostly reversible, as the clearance of *C. odorata* in this study resulted in previously invaded sites showing similar assemblages to the control sites after clearance (Fig. 4). The different results from the two sampling methods show the immediate positive impact of clearing of *C. odorata* on native spider communities. Higher abundance is observed in recently cleared sites for pitfall trap data in comparison to sites that have been cleared for a longer duration (Fig. 6b). However, the converse trend is observed for the vegetation beating data which targeted spiders that inhabited *C. odorata*, with higher abundance observed in sites cleared for a longer duration (Fig. 6a). Furthermore, the pitfall trap data supported this trend, highlighting the rapid positive impact of clearing *C. odorata* and the importance of clearing this invasive. Of greatest importance is the result that spider communities do re-establish after the weed has been cleared, as demonstrated by the high index of similarity to the control sites. Indeed, Gratton & Denno (2005) showed that removal of the invasive plant by herbicide application resulted in the rapid return of native plant species that are associated with an arthropod assemblage indistinguishable from that in uninvaded sites. The importance and positive impact of *C. odorata* clearance is demonstrated by the higher diversity in cleared sites in comparison to sites that have been invaded for longer durations (Table 1).

Conclusion

Chromolaena odorata invasion resulted in a reduction of numerically dominant spiders, and changes in spider assemblage patterns, species richness and diversity. This is probably the result of disruption of food web interactions and flow of energy in invaded habitats (Tallamy 2004). This, in turn, may cause a trophic cascade and, in turn, may affect the density and diversity of insectivorous birds and other high order consumers (Levine *et al.* 2003; Greenwood *et al.* 2004). Invasive plant communities may not be functionally equivalent to the native plant communities in respect to arthropod food webs (Gratton & Denno 2005). Therefore, the return of spider communities to the cleared sites in comparable proportions to control sites not only restores the native arthropod diversity but also recreates the trophic structure (Gratton & Denno 2005).

The findings of this study are consistent with the widely held view that vegetation structure is indeed of primary importance in determining the composition of spider assemblages (Wise 1993; Knops *et al.* 1999). They also support the observation that re-establishment of native vegetation in areas that have been altered or dominated by an invasive plant, can result in the restoration of a significant component of the biodiversity (Palmer, Ambrose & Poff 1997), making the effects of invasive alien plants reversible, even for sensitive indigenous taxa (Gratton & Denno 2005). Crucially, the

variations in the impacts of different invasion durations of *C. odorata* found in this study show the great importance of incorporating temporal variables when assessing the impacts of invasive plants. The population size of invasive species vary over time together with environmental factors, and the full effects of the invader might not be seen for a considerable length of time after the initial invasion; thus, the chronic long-term effects of invasive plant species represent the actual outcomes of the species invasion (Strayer *et al.* 2006).

Management applications

Alien clearance is an essential and invaluable management tool. However, the small, but lingering differences between the native and the cleared habitats suggest that other features of the habitat may be affected by the invasion and clearance operations. That two families, namely Cyrtaucheniidae and Uloboridae, did not return after invasion needs to be the focus of more specific conservation strategies. There are a substantial number of programmes that aim to control alien invasive plants but very little is known about how biodiversity recovers after alien plant removal. Samways *et al.* (2005) showed that the removal of alien invasive plants benefits biodiversity with immediate effects, highlighting that effective management can be utilized to directly benefit irreplaceable biodiversity. Similarly, the clearing of *C. odorata* promotes the re-establishment of native spider assemblages within a short time-scale. Therefore, clearance of this notorious weed, together with follow-up treatments as well as the prevention of invasion of new areas, should be promoted in order to conserve the native biota. Our data can be used to inform policy-makers as to the effects of aliens and the value of restoration programmes for biodiversity.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Spider species and families captured.

This material is available as part of the online article from:

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