

Herbivores, but not other insects, are scarce on alien plants

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Abstract Understanding how the landscape-scale replacement of indigenous plants with alien plants influences ecosystem structure and functioning is critical in a world characterized by increasing biotic homogenization. An important step in this process is to assess the impact on invertebrate communities. Here we analyse insect species richness and abundance in sweep collections from indigenous and alien (Australasian) woody plant species in South Africa's Western Cape. We use phylogenetically relevant comparisons and compare one indigenous with three Australasian alien trees within each of Fabaceae: Mimosoideae, Myrtaceae, and Proteaceae: Grevilleoideae. Although some of the alien species analysed had remarkably high abundances of herbivores, even when intentionally introduced biological control agents are discounted, overall, herbivorous insect assemblages from alien plants were slightly less abundant and less diverse compared with those from indigenous plants – in accordance with predictions from the enemy release hypothesis. However, there were no clear differences in other insect feeding guilds. We conclude that insect assemblages from alien plants are generally quite diverse, and significant differences between these and assemblages from indigenous plants are only evident for herbivorous insects.

Key words: biological control agent, biological invasions, Cape Floristic Region, enemy release hypothesis, insect herbivory, trophic cascade.

INTRODUCTION

Several factors that contribute to the success of alien plants involve their associated insect faunas (Rejmánek *et al.* 2005). According to the enemy release hypothesis, the success of invasive alien plants is partly attributable to their release from natural enemies (Wolfe 2002; Siemann & Rogers 2003). However, numerous other mechanisms also encourage successful establishment. Insect pollinators can become preferentially attracted to alien plants, and fewer pollinators on indigenous plants will result in reduced seed output (Richardson *et al.* 2000; Traveset & Richardson 2006). The presence of aliens can also indirectly increase the levels of seed predation on indigenous species (Ghazoul 2002; Traveset & Richardson 2006), and herbivory on aliens can cause allelopathic reactions that affect neighbouring indigenous plants (Thelen *et al.* 2005). A recent study suggested that generalist alien herbivores, in particular, are likely to promote further plant invasion (Parker *et al.* 2006).

Several studies have shown that the richness (and often the abundance) of insects on plants is lower in

the plants' introduced range than in their original range, resulting in lower herbivory levels in the former (Strong *et al.* 1984 and references therein; Fenner & Lee 2001; Hierro *et al.* 2005; Cripps *et al.* 2006). Fewer studies have compared the insect diversity and abundance on alien and indigenous plants at a given location (see McEvoy 2002; Tallamy 2004). Of the available studies (see reviews in Colautti *et al.* 2004; Harris *et al.* 2004), some suggest that insect abundance and diversity are indeed lower on alien plants compared with their indigenous relatives growing in proximity. This presumably results in a relatively greater herbivore pressure on the indigenous species (Olckers & Hulley 1991; Dietz *et al.* 2004), and arguably increases the ability of the non-indigenous species to invade. On the other hand, if the species considered are very closely related, herbivory tends to be heavier on the non-indigenous plants (Agrawal & Kotanen 2003; Frenzel & Brandl 2003). Given the close similarity between the plants, the aliens become appropriate hosts for the specialized herbivores of their indigenous relatives, which, in turn, are better defended against these specific herbivores owing to long-term coevolutionary processes (Futuyma *et al.* 1995; Maron & Vilà 2001). In these cases, the 'biotic resistance hypothesis' (Elton 1958; Mack 1998) apparently takes precedence over the enemy release hypothesis (see Mitchell *et al.* 2006).

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From an interregional perspective, the enemy release hypothesis may be better supported where donor and recipient floras have been separated for a long period, and where indigenous and alien plants are distantly related. Herbaceous floras of the northern landmasses (North America and Eurasia) have exchanged species repeatedly during the Tertiary, and many species have very close relatives across the ocean. Therefore, one may expect 'biotic resistance' to dominate (see Agrawal & Kotanen 2003).

At the other end of the spectrum, the tree floras of Australia and South Africa are both characterized by high-generic-level endemism (Elliot & Jones 1980; Goldblatt & Manning 2000), and the separation between closest relatives on the two sides of the Indian Ocean can in most cases be dated back to the break up of Gondwanaland, or to fairly old long-distance dispersal events (e.g. Sytsma *et al.* 2004). Therefore, it might be predicted that enemy release would be common, with few herbivores gaining access to the alien species. To test this prediction, we compare the insect assemblages from Australasian alien trees in the Cape Floristic Region of South Africa with those from their indigenous relatives, in terms of species richness and abundance.

The insect faunas of several alien plant species in southern Africa have been surveyed. Insect herbivore diversity on aliens is typically lower than that on related or ecologically equivalent indigenous plants (Southwood *et al.* 1982; Olckers & Hulley 1991). Several studies have also compared the diversity of insects dwelling in the soil, in leaf litter or on herbaceous plants below indigenous southern African vegetation and below alien trees, with variable results (Samways & Moore 1991; Samways *et al.* 1996; Steenkamp & Chown 1996; French & Major 2001; Ratsirarson *et al.* 2002). However, there has been no systematic attempt to compare the insect faunas living on indigenous and alien plants to test the enemy release hypothesis. Our objectives were therefore (i) to test whether herbivore assemblages show patterns consistent with predictions of the enemy release hypothesis; (ii) to assess whether differences in insect assemblage metrics perpetuate up the food chain – i.e. are insect predators and parasitoids also underrepresented on alien trees; and (iii) to assess the proportional representation of introduced biological control agents on these species.

MATERIALS AND METHODS

Study area and taxa

The south-western part of the Cape Floristic Region is characterized by mediterranean-type climate, with

cool rainy winters (June – August) and dry hot summers (December – February). In winter, temperatures commonly drop below freezing on mountain peaks, but the lowlands are generally frost free. The region is largely covered by fynbos vegetation (a species rich, fire-prone shrubland, dominated by Proteaceae, Ericaceae and Restionaceae), but river valleys tend to be lined with taller vegetation, including a variety of tree taxa, locally forming forest pockets (Goldblatt & Manning 2000). However, most of the lowlands have been transformed for agriculture or development, and are extensively invaded by alien plants (Rouget *et al.* 2003). Invasive alien plants from several taxonomic groups co-occur locally (Richardson *et al.* 1992; Henderson 1998; Thuiller *et al.* 2006). Moreover, alien species often co-occur with indigenous relatives, in several cases classified as con-generics (see Goldblatt & Manning 2000). A large proportion of the woody species of plant invaders in the Cape are of Australasian origin, most often originating in the south-western or south-eastern parts of Australia, which have climatic conditions similar to those found in the Cape (Richardson & Thuiller 2007). Three such taxa (Fabaceae: Mimosoideae; Myrtaceae; and Proteaceae: Grevilleoideae) are considered here.

Acacia is the largest genus in the legume subfamily Mimosoideae, with *c.* 1200 species worldwide in its broadest sense (but see classification suggested by Maslin *et al.* 2003). Two regions are particularly rich in species: Africa, where acacias are dominant trees in savanna vegetation (subgenera *Acacia* and *Aculeiferum*), and Australia, where the genus occurs in a variety of environmental conditions (subgenus *Phyllodineae*). The separation between African and Australian acacias is thought to have happened *c.* 20 Myr ago (Lavin *et al.* 2005). The Cape Floristic Region is poor in indigenous acacias, with only one species (*A. karroo*) being common. On the other hand, numerous phyllodinaceous Australian species are important invaders (Richardson *et al.* 1992). The Australian acacias studied here are either closely related to, or are themselves, species of commercial value, and so only reproductive feeders have been introduced as classical biological control agents (Impson & Moran 2004). These include a seed weevil (*Melanterius servulus*) and a cecidomyiid fly (*Dasineura dielsi*) to control *Acacia cyclops*; the bud-galling wasp (*Trichilogaster acaciaelongifoliae*) and the seed weevil (*Melanterius ventralis*) to control *Acacia longifolia*; and the seed weevil (*Melanterius maculatus*) to control *Acacia mearnsii*. The *Trichilogaster* wasps and the cecidomyiid fly have dispersed readily and are widely established in South Africa, and the *Melanterius* seed weevils, although less widely spread, are abundant and effective in and around their release sites. The biological control agents all have the capacity to reduce the reproductive performance of attacked trees, limiting

propagule pressure and the rate of spread of the species (McGeoch & Wossler 2000; Impson *et al.* 2004).

In Myrtaceae, the genus *Metrosideros* has a largely Australasian-Pacific distribution, extending as far east as Hawaii. A total outlier is *M. angustifolia*, indigenous to the Cape Floristic Region, where it is an important component of riparian scrub communities (Galatowitsch & Richardson 2005). It has been implied that this species may not truly belong in the genus *Metrosideros*, but represents the result of a rather early dispersal event during the Tertiary, from the Australasian core area of distribution of the Myrtaceae (Sytsma *et al.* 2004). However, no molecular analyses have considered the Cape species as yet. Recently, a New Zealand species from the same genus, *M. excelsa* (the New Zealand Christmas tree), has become established in the Cape (Rejmánek *et al.* 2005), but no biological control has been attempted yet. Another species of Myrtaceae, highly invasive in sandy areas in the Cape, is the Australian myrtle (*Leptospermum laevigatum*; Richardson *et al.* 1992). A leaf-mining moth (*Parectopa thalassias*) and a bud-galling cecidomyiid fly (*Dasineura* sp.), have been introduced to control this species (Gordon 1999a). The largest genus of Myrtaceae, and the Australasian genus with by far the highest number of introductions in South Africa is *Eucalyptus*, 150 species of which have been cultivated in the country at some stage. However, few of these have become invasive (Forsyth *et al.* 2004), and given the wide use of eucalypt wood, control is effected by mechanical clearing, rather than biological control.

For the third study group included here (the Proteaceae subfamily Grevilleoideae), it has been suggested that the disjunction between Australasian and African taxa could date back to the split of Gondwanaland, during the Mesozoic. Currently, the subfamily is represented by a single indigenous species on the African continent: *Brabejum stellatifolium* (the wild almond). Morphologically, the genus *Xylomelum* (woody pears) from south-western Australia is similar to *B. stellatifolium*, but molecular studies do not support a close relationship between the two genera, *Macadamia* (from eastern Australia and Celebes to New Caledonia) being more closely related (Hoot & Douglas 1998). Among the invasive species, the most widespread are *Hakea sericea* (the silky hakea), *H. drupacea* (= *H. suaveolens*) and *H. gibbosa* (Richardson *et al.* 1992). In controlling the silky hakea, two introduced insect species have met with some success: the hakea fruit weevil, *Erytenna consputa*, and the hakea seed moth, *Carposina autologa* (Gordon 1999b). Subsequent to 2005, two additional biological control agents, the stem-boring beetle, *Aphenasium australe*, and the flower bud feeding weevil, *Dicomada rufa*, have been released (A.J. Gordon, unpubl. data 2006). However, the spiny habit of these three *Hakea* species

makes them morphologically distinct from *Brabejum*. Non-invasive, but broadly cultivated and locally naturalized, are the broad-leaved species *H. salicifolia* (Richardson *et al.* 1987), and a few *Banksia* species (Honig *et al.* 1992), these being considered here.

Collections and sample processing

Insects were collected in 2005 by sweep-netting five randomly selected plants (50 hits per plant) in medium to large populations (a minimum of 20 plants) representing largely homogeneous monospecific patches. All collections were done during late mornings with clear sky, to minimize variation due to weather conditions. Two localities per species were sampled in July, to assess geographical variation, and one locality for each species was re-sampled in December (using different plants), to consider potential seasonal variation. Therefore, 15 trees of each plant species, from two different sites (Fig. 1) were sampled. At all sites, a few variables were noted (distance from running water, slope at the 100 m scale), and other environmental variables (mean annual and seasonal precipitation and temperatures) were derived from available climate data sets (Schultze 1997).

Insect individuals were identified as morphospecies (see Oliver & Beattie 1996) and classified into three guilds roughly corresponding to different trophic levels (herbivores, predators and parasitoids, and detritivores), based on the predominant feeding strategy for each family or subfamily. A crude measure of biomass based on insect length, width and height was also considered, but this measure was highly variable and no significant relationships were observed (results not presented).

Analyses

The insect data were analysed using generalized linear mixed-effects models. To allow for statistical comparisons between models, the models were fitted using a Laplacian approximation (function 'lmer' in the Matrix library in the statistics package R (R Development Core Team 2006)). The response variable was species richness or abundance, fixed effects were season (summer or winter) and whether the plant species sampled was indigenous (yes or no), and random effects were plant family and plant species nested within family. Analyses were repeated using only sites that were sampled in both winter and summer to remove possible biases owing to an interaction between site and season. As the results obtained were qualitatively similar, we only present the results from analyses of the complete data set with all sites included. Poisson errors were used to model species

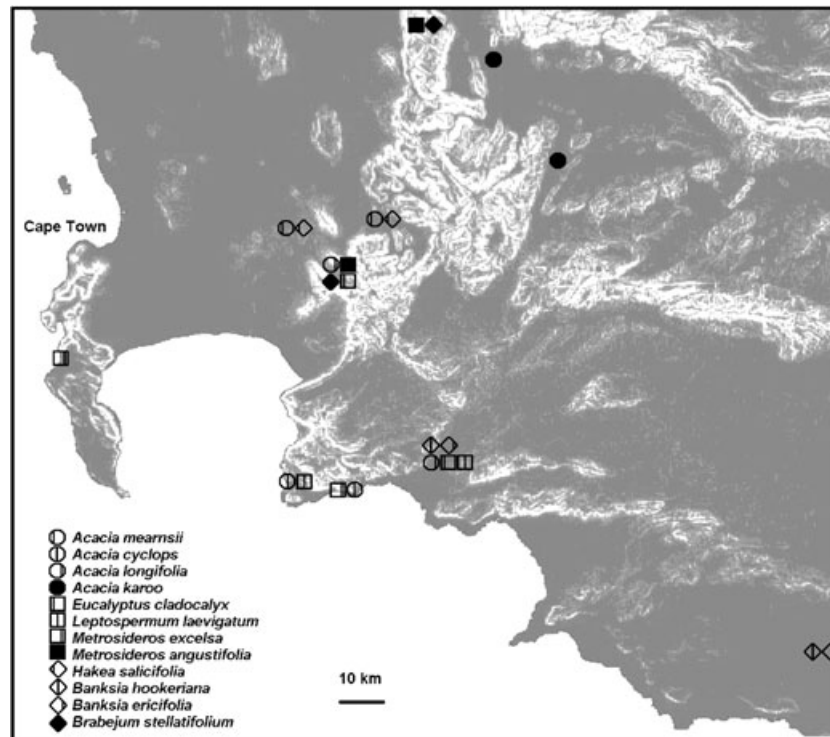


Fig. 1. Localities sampled for insect species richness and abundance on indigenous and alien plant species in the Western Cape, South Africa. Steep altitudinal gradients are indicated in white.

richness since species richness values are count data, and there was no evidence of under- or over-dispersion (estimated scale parameters for the fitted models were approx. 1). For species abundance (also count data), a log-link function with variance increasing with the square of the mean was used (as the estimated scale parameters for models fitted with Poisson errors were greater than 1.5). These analyses were repeated for the different insect guilds.

Differences in insect diversity and abundance between sites could not be thoroughly explored, as most sites contained only one or two of the plant species investigated. However, it was necessary to test whether any of the observed differences could be due to alien and indigenous plants occurring at different sites. For this, environmental variables at the sites were compared using Wilcoxon rank sum test.

To examine the importance of the phylogenetic component in our analysis, we tested the significance of the random effects. Models with species nested within family as a random effect were compared using an ANOVA to models with only species or only family as a random effect.

RESULTS

At the sampling sites, indigenous trees tended to be closer to water than alien trees ($P = 0.026$), and, on

average, indigenous species were sampled at higher elevation sites ($P = 0.0056$, approx. 200 m) that were colder in winter ($P = 0.0015$, approx. 1.5°C) and suffered more frosts ($P = 0.0012$, 30 days *vs.* 10 days). There were no significant differences in mean annual precipitation ($P = 0.366$) or summer temperature ($P = 0.088$) between the sites occupied by indigenous and alien species, and the local slopes where the alien species and indigenous species were sampled also did not differ ($P = 0.57$).

In total, 3244 insect individuals were collected and assigned to 315 morphospecies. Both insect abundance and species richness varied substantially between plant species, and in some cases within plant species (e.g. insect abundance varied greatly between samples from *A. cyclops*) (Fig. 2, Table 1). Overall, insect abundance was greater on indigenous plants than on alien plants, but species richness was not significantly different. However, for the summer samples both insect abundance and species richness were greater in samples from indigenous plants. When analysing insect feeding guilds separately, the abundance and species richness of herbivores were always significantly higher on indigenous than on alien plants, but at other trophic levels (i.e. predators/parasites or detritivores) the differences were smaller or season-dependent (Table 1). Although there tended to be fewer predators and parasites per sample, species richness and abundance values for the samples were

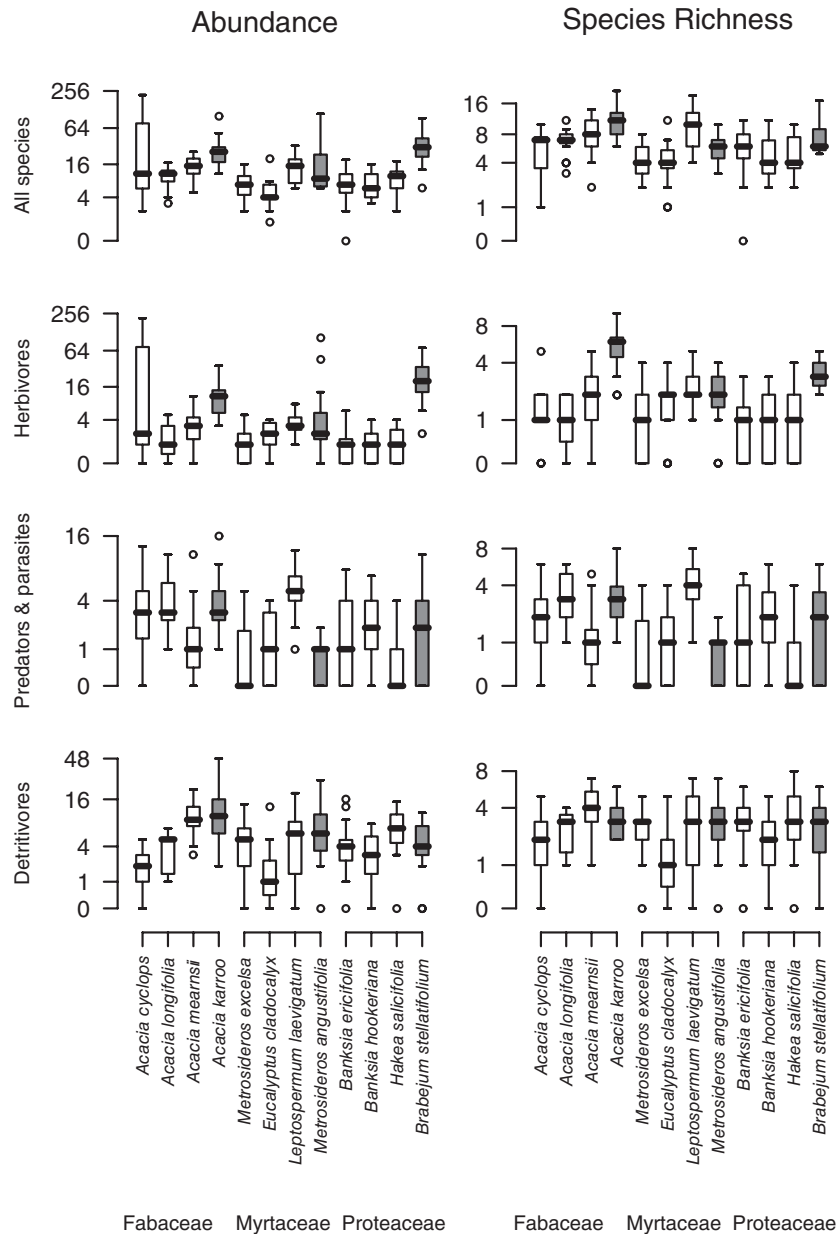


Fig. 2. Differences in species richness and abundance between the insect samples collected on introduced (white bars) and native (grey bars) plant species ($n = 15$). The bold lines show the median, the boxes the quartile ranges, and the lines show either 1.5 times the interquartile range or the point furthest from the median, whichever is less. Outliers outside this range are plotted individually.

broadly comparable for the three guilds (Fig. 2), and so the statistical tests used should be similar in power.

Less than one percent of the insect individuals collected on alien plants belonged to species purposefully introduced as biological control agents (11 individuals of *P. thalassias*, six *D. dielsi*, five *T. acaciaelongifoliae*, two *Dasineura* sp. and one *Melanterius acaciae*). However, over 700 individuals of the acacia psyllid

(*Acizzia uncatoides*) were collected from *A. cyclops* (making it the most abundant species in our collections), and one individual of *Gonipterus* sp. (Curculionidae) from *Eucalyptus*. Both these species are host-specific herbivores that were accidentally introduced from Australia. Most of the abundant herbivore species from alien plants are apparently indigenous to southern Africa, although precise identification for most of them was not possible.

Table 1. Analyses of abundance and species richness for all insects, and separately for three insect feeding guilds

Guild	Parameter	Fixed effects			Random effects		Interpretation
		ind:sea	sea	ind	fam	species	
All	Richness	**	na	na	†	***	Indigenous plants have higher insect richness in summer, but in winter indigenous and alien species do not significantly differ
	Abundance	†	*	*	†	**	Indigenous plants have higher insect abundance than alien plants, and insect abundance is higher in summer than in winter
Herbivores	Richness	†	‡	**	†	***	Indigenous plants have much higher species richness at both seasons (predicted 1.4 vs. 3.4). Although the species richness was lower in winter, this was not a significant effect ($P = 0.052$)
	Abundance	†	*	**	†	***	Indigenous plants have higher herbivore abundance than alien plants, and insect abundance is higher in summer than in winter
Predators and parasites	Richness	*	na	na	†	***	Indigenous plants have more clear seasonal patterns than alien plants
	Abundance	†	†	†	†	†	
Detritivores	Richness	†	†	†	†	***	
	Abundance	†	†	‡	†	***	

Significance: † $P > 0.1$, ‡ $0.1 > P \geq 0.05$, * $0.05 > P \geq 0.01$, ** $0.01 > P \geq 0.001$, *** $P < 0.001$. The effects of the plants insects were collected from (indigenous vs. alien) are coded as 'ind', the effects of season as 'sea', and the interaction between these two factors as 'ind:sea'; 'fam' indicates the effect of plant families. The fixed effect of species is confounded by site, and may partially explain the high significance level observed.

The results were broadly consistent across the three plant families (family as a fixed effect was never significant), but there were clear species differences (Table 1).

DISCUSSION

Our results can be summarized in three statements: (i) more species and individuals of insect herbivores occur on indigenous plants; (ii) when extending analyses to all insects, differences between indigenous and alien plants are not immediately obvious, and need to be qualified in terms of seasonal representation; and (iii) biological control agents are not particularly abundant, and could be completely overlooked in a superficial assessment. We explore each of these ideas in turn.

Fewer herbivores on aliens

While direct support for the enemy release hypothesis can only be provided through an assessment of herbivore damage on plants and how this damage affects a

plant's fitness (Keane & Crawley 2002), our study confirms that alien plants support fewer herbivore species than do related indigenous species (Fig. 3). Nevertheless, variation among species is substantial. Some alien species supported as many insect herbivore individuals as their indigenous relatives. Of course, not all of these insects were necessarily feeding on the plant where they were collected, but actual feeding was observed in over 20 species, including the four most abundant herbivores. Certainly, once an indigenous herbivore manages the transition to feeding on an alien plant (particularly a widespread invasive one) the alien plant can become an important resource, with large amounts of biomass available and little competition from other herbivores. The indigenous alydid bugs in the genus *Zulubius* have already been recognized as important control agents of *A. cyclops* (Holmes & Rebelo 1988), but this genus was not recorded in our collections.

Many other factors have been implicated in determining insect diversity and abundance on plants (Strong *et al.* 1984), and can partly account for the large amount of variation in our data. In both indigenous and alien species, leaf structural traits (Peeters 2002) are likely to be important. Among the indig-

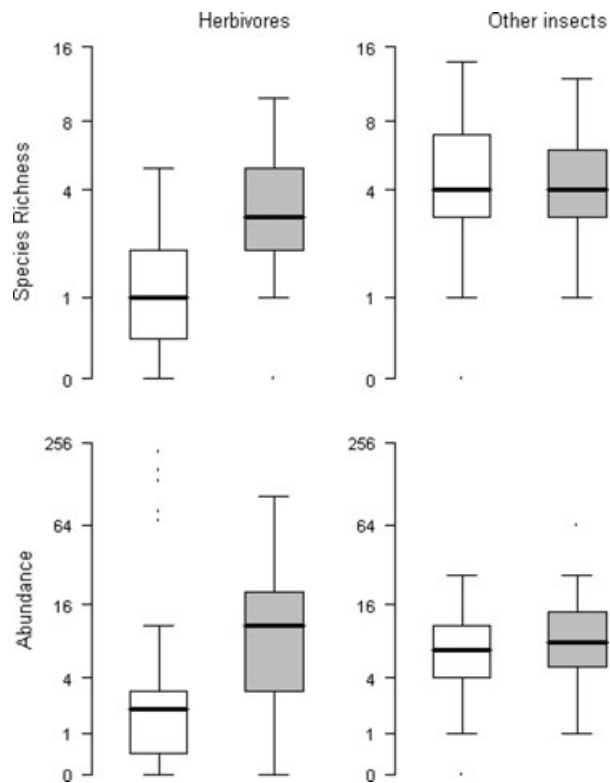


Fig. 3. Summary of results, showing different patterns in herbivores and other insects. Species richness and abundance of herbivores is lower on introduced host plants (white) than native host plants (grey), but the species richness and abundance of other trophic levels is not affected by the origin of the host plant.

enous species in our study, a very likely effect was range size, with the widespread *Acacia karroo* (cf. Krüger & McGavin 1998) having a much richer herbivore fauna than the two localized endemics *Metrosideros angustifolia* and *B. stellatifolium*. Among aliens, time since introduction has been shown to be an important variable in explaining herbivore diversity, indigenous herbivores being accumulated over time (Strong *et al.* 1984). However, most of the Australasian species considered here were introduced in the middle of the 19th century (see Wilson *et al.* 2007), so there was too little variation in residence time to use this as an explanatory variable.

A few potential caveats need to be considered in interpreting our results as support for the enemy release hypothesis. The selection of the alien species in question is a non-random selection from the pool of Australasian aliens, a choice essentially made by humans (see Thuiller *et al.* 2006). The success of establishment and spread of these species may have been related to serendipitous factors (such as being introduced with fewer host-specific fungi or insects) as well as more fundamental factors (like having a higher climatic suitability and lower propensity for

herbivory). Species, or rather species introductions, that suffered high herbivory may either simply have not established or, as high levels of damage would make them unattractive as ornamental or crop species, they may not have been widely planted.

No clear difference in other insects

Trees, irrespective of their origin and antiquity in a given system, represent structures which will elicit attention from flying insects. In particular, many insect predators are active fliers and will colonize any available surface or structure (Edwards & Sugg 1993). Therefore, one can expect alien trees to be colonized by predaceous and parasitic insects from neighbouring indigenous vegetation. Populations of predaceous and parasitic insects will be locally sustainable insofar as alien tree stands are habitat for their prey or hosts, but it may be common that populations on alien trees function as 'sinks'. Nevertheless, our finding of no clear differences in predator/parasitoid abundance between alien and indigenous plants was not a predictable result, given the large number of host-specific parasitoids often associated with host-specific herbivores (Stireman & Singer 2003). The clearer seasonal patterns in predaceous/parasitic insects from indigenous plants (Table 1) suggest that either some parasitoids also feed on pollen or nectar in their adult phase, or that many of them are associated with herbivores from plant reproductive structures (virtually all plant species studied here flower in summer; Goldblatt & Manning 2000; Henderson 2001).

Detritivores are similar to generalist herbivores in the sense that they exploit various types of plant matter largely irrespective of species identity, and the lack of clear differences here (Table 1) is less surprising.

Control agents

Among the herbivores that increase numerically (as adults) during the flowering season are those classical biological control agents that are reproductive feeders (the majority in the systems studied here). However, even in our summer collections, control agents represented a small proportion of all insects, or even of insect herbivores taken alone. Some control agents considered quite successful in reducing seed production in the Cape (e.g. *M. servulus*; Impson *et al.* 2004) were totally absent from our collections, while the only species that appeared fairly abundant, and was also present in winter (*P. thalassias*), is not considered particularly successful (Klein 2000). Furthermore, the control agent species which ranked second in our collections (*T. acaciaelongifoliae*) was accompanied by large numbers of indigenous hyperparasitoids (e.g.

torymid wasps), also recorded in a dedicated study on the food chains initiated by the introduction of this species in South Africa (R. Veldtman, unpubl. data 2006). However, the patterns observed may appear significantly different for different sampling seasons.

In the case of *D. dielsi* on *A. cyclops* and *T. acaciaelongifoliae* on *A. longifolia*, the galling these agents cause has led to the creation of extensive novel food webs (C. Kleinjan and R. Veldtman, respectively, unpubl. data 2006). Classical biological control agents which are abundant, but have little immediate effect on target plant density, may have important indirect effects. Particularly when introducing reproductive feeders, the risk of adverse indirect effects should be assessed (e.g. Louda *et al.* 1997).

CONCLUSION

The clearest result of our study relates to the different patterns observed for herbivores and for other insects. The overall patterns in insect abundance and diversity illustrated here may be partly due to differences between the sites where indigenous and alien plants were located – a problem that could be solved by more extensive replication. In this study, the requirement of sufficiently large monospecific plant stands forced us to collect the two categories of plants at different sites, with aliens occurring more extensively in the lowlands, and indigenous species persisting predominantly at higher altitudes. Harsher winter climate at the inland, high-altitude sites where indigenous plants were sampled may contribute to counter-balancing the lower diversity and abundance that could be expected on alien plants, given the shorter period of time that insects have had to become associated with them. This would, however, not explain guild differences.

Another important point relates to the choice of phylogenetic controls in indigenous–alien comparisons. The plant species chosen here have diverged too long ago for most intrafamilial relationships to be meaningful to the herbivores, and the families plants belonged to were less important than variation within families (Table 1). This likely contributed to the support we find for the enemy release hypothesis. Indeed, to most indigenous South African herbivores, most alien plants considered here had no recognizable relative.

The picture presented here is one of aliens – both plants and their control agents – being better integrated into the environment than might have been expected. The alien trees becoming dominant across many landscapes in the Cape Floristic Region (Richardson *et al.* 1992) can harbour rich and abundant insect faunas. Of course, this does not exclude grave reductions in insect population sizes, or even

species extinctions as a consequence of the plant invasions. Insects introduced for biological control were not found to be dominant, and the gall-formers in particular appear to support their own sets of parasitoids. While we do not debate the success of introduced control agents in limiting alien plant spread, the success of indigenous insects in helping or hindering this control may be underrated.

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