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# The role of exotic plants in the invasion of Seychelles by the polyphagous insect *Aleurodicus dispersus*: a phylogenetically controlled analysis

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**Abstract** The accidental introduction of the spiralling whitefly, *Aleurodicus dispersus* Russell (Homoptera: Aleyrodidae) to Seychelles in late 2003 is exploited during early 2005 to study interactions between *A. dispersus*, native and exotic host plants and their associated arthropod fauna. The numbers of *A. dispersus* egg spirals and pupae, predator and herbivore taxa were recorded for eight related native/exotic pairs of host plants found on Mahé, the largest island in Seychelles. Our data revealed no significant difference in herbivore density (excluding *A. dispersus*) between related native and exotic plants, which suggests that the exotic plants do not benefit from 'enemy release'. There were also no differences in predator density, or combined species richness between native and exotic plants. Together these data suggest that 'biotic resistance' to invasion is also unlikely. Despite the apparent lack of differences in community structure significantly fewer *A. dispersus* egg spirals and pupae were found on the native plants than on the exotic plants. Additional data on *A. dispersus* density were collected on Cousin Island, a managed nature reserve in which exotic plants are carefully controlled. Significantly higher densities of *A. dispersus* were observed on Mahé, where exotic plants are abundant, than on Cousin. These data suggest that the rapid invasion of Seychelles by *A. dispersus* may largely be due to the high proportion of plant species that are both exotic and hosts of *A. dispersus*; no support was found for either the 'enemy release' or the 'biotic resistance' hypotheses.

**Keywords** *Aleurodicus dispersus* · Biotic resistance · Enemy release · Invasion · Seychelles

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## Introduction

The threats posed to agricultural and natural ecosystems by invasive species are well known. Invasive species have been shown to modify ecosystem structure and function (Christian and Wilson 1999; Mack et al. 2000), reduce biodiversity (Wilcove et al. 1998; Heidinga and Wilson 2002), and negatively affect fishery and crop yields (Pimentel et al. 2005; Colautti et al. 2006). Despite the problems caused by invasive species there is little consensus on which ecological processes influence invasion success. Here we exploit the recent (late 2003) accidental introduction of a highly invasive herbivorous insect, *Aleurodicus*

*dispersus* Russell (Hemiptera: Aleyrodidae) to Seychelles in order to better understand which ecological processes may constrain the spread of *A. dispersus*.

Since 1962 *A. dispersus* has spread rapidly around the tropics from its native range of Central America and the Caribbean (Russell 1965; Waterhouse and Norris 1989; Ramani et al. 2002). Typically *A. dispersus* populations increase dramatically during the early stages of an invasion and then stabilise after a number of years at levels many orders of magnitude higher than in their native range (Ramani 2000; Ramani et al. 2002). Fortunately biological control is easily achieved using a variety of specialist natural enemies (Kumashiro et al. 1983; Neuenschwander 1996; D'Almeida et al. 1998; Mani et al. 2004). The results of these studies and the observation that *A. dispersus* is generally rare in its native range (Russell 1965; Waterhouse and Norris 1989), suggest that 'enemy release' is important in determining the success of *A. dispersus* in areas where its natural enemies are absent.

The enemy release hypothesis argues that invasive species are successful because they have escaped the predators, parasites, and pathogens that help regulate their populations in their native range (Elton 1958; Keane and Crawley 2002; Mitchell and Power 2003; Agrawal et al. 2005). Enemy release is intuitively appealing and is often cited as the most important factor determining invasion success although the evidence is often little better than anecdotal. Indeed, a number of recent studies of plant invasions have either failed to find supporting evidence or have shown that native herbivores control exotic plants more effectively than previously thought (Colautti et al. 2004; Levine et al. 2004; Parker et al. 2006). In contrast, the 'biotic' or 'ecological' resistance hypothesis argues that biodiversity helps buffer against invasion because invading organisms are more likely to interact negatively with existing community members via competition and predation in species rich communities (Elton 1958; Levine et al. 2004). Evidence for the 'biotic resistance' hypothesis shows that more diverse communities can resist invasion (Anderson and Inouye 2001) but that this process is rarely strong enough to prevent establishment, or lead to the exclusion of an invading species and instead acts to regulate population size (Levine et al. 2004).

An island wide parasitism assay (Hazell et al. unpublished data) and observations made during this study indicate that none of *A. dispersus*'s natural enemies had become established at the time of the study. Therefore this study is designed to test which factors limit the spread of *A. dispersus* in the absence of its natural enemies. Anecdotal evidence from Seychelles residents (T. Vel, pers. comm.) suggests that *A. dispersus* prefer to attack exotic rather than native plant species. Few of the exotic plant species in Seychelles originate from the Caribbean, the native range of *A. dispersus*, while a number of the native coastal lowland species have near pan-tropical distributions and are found within the home range of *A. dispersus* (Robertson 1989). In consequence, any preference for exotic hosts is unlikely to be related solely to evolved associations between *A. dispersus* and its hosts. Instead, this pattern might be generated by a combination of enemy release and biotic resistance if exotic host plants support smaller arthropod communities and as a result offer weaker biotic resistance to invasion.

To test this hypothesis we performed a phylogenetically controlled analysis of arthropod and whitefly densities on eight pairs of related native and exotic host species in Seychelles. The potential effects of host familiarity, whitefly or host adaptation, and taxonomic bias were minimised by selecting two groups of related native and exotic host plants, all of which are present within the wider region. Accordingly, any differences in whitefly density observed between the native and exotic plant groups used in this study should be attributable to differences in 'biotic resistance', possibly due to variations in community structure as a result of enemy release on exotic plant species.

## Materials and methods

*Aleurodicus dispersus* was common on every island visited (Mahé, La Digue, Praslin, Cousin, Cousine; S. Hazell, unpublished observations) and was also reported anecdotally from several other islands (Aride and Silhouette). Sampling was conducted on the main island of Seychelles, Mahé (4°45′S, 55°30′E, area 155 sq. km) during March and April 2005. A total of eight sites were identified around the

coastal fringe of Mahé at which two or more of the target plants were present. At each site between one and ten plants were selected on an ad hoc basis (due to wide variation in the availability and accessibility of plants at different sites). A total of between 15 and 29 plants (Table 1) were examined from between two and five sites per species. For each plant a total of 20 leaves were selected haphazardly and examined. The numbers of *A. dispersus* egg spirals and pupae, and the numbers of individuals of putative predators and herbivores were recorded per leaf and then averaged for each plant. Arthropods assigned to the predator group included species thought likely to be whitefly predators e.g. ants (Hymenoptera: Formicidae), ladybirds (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae), and spiders (Araneae) whereas those assigned to the herbivore group were almost entirely plant feeding Hemiptera (e.g. Aleyrodidae (excluding *A. dispersus*), Cicadellidae, Cixiidae, Coccoidea) or galling insects of uncertain affinity.

The host plant pairs chosen were related at least at the family level (and in three cases were in the same genus) to eliminate the potential confounding effects of taxonomic bias. Exotic plant species that are either defined as invasive, or have become naturalised and survive well when not cultivated were used (Robertson 1989). To ensure that the Seychelles population of *A. dispersus* would have had prior experience of the plants in the native plant group (thereby reducing the likelihood that herbivore choice could skew our results); native plants were only selected if they are widely distributed throughout the region (Robertson 1989). Samples were also collected from Cousin Island (4°20′S, 55°40′E, area 27 ha), 45 km North West of Mahé but only 2 km from the nearest heavily infested island, Praslin. All of the native plants except *Premna serratifolia* are found on Cousin Island. Invasive plants are actively removed on Cousin but eight small bushes of *Quisqualis indica* were located. Leaf size was recorded for nine leaves from plants collected on Mahé, three each from three plants per species.

### *Statistical analysis*

The mean numbers of *A. dispersus* egg spirals, pupae, predators, and herbivores per leaf were controlled for leaf size and compared between the native and exotic plant group using Wilcoxon matched pairs tests. The mean numbers of morphospecies present per leaf were also compared using Wilcoxon matched pairs tests. The mean numbers per leaf of egg spirals and pupae were compared between islands for those plant species present on both islands using Wilcoxon

**Table 1** Showing the native/exotic species pairs by family and giving the number of samples from Mahé and Cousin Island and mean leaf area ($mm^2$) for each species

| Family | Pair | Status | Species | Leaf area ($mm^2$) | *N* Mahé | *N* Cousin |
|---|---|---|---|---|---|---|
| Malvaceae | 1 | Native | *Hibiscus tiliaceus* L. | 21285 | 20 | 10 |
| | | Exotic | *Hibiscus rosa-sinensis* L. | 3002 | 20 | 0 |
| Euphorbiaceae | 2 | Native | *Euphorbia pyrifolia* Lam. | 1909 | 15 | 10 |
| | | Exotic | *Acalypha wilkensia* Müll. Arg. | 13382 | 20 | 0 |
| Moraceae | 3 | Native | *Ficus lutea* Baker | 26609 | 20 | 16 |
| | | Exotic | *Ficus benjamina* L. | 1558 | 29 | 0 |
| Combretaceae | 4 | Native | *Terminalia catappa* L. | 30633 | 20 | 10 |
| | | Exotic | *Quisqualis indica* L. | 4002 | 20 | 8 |
| Convolvulaceae | 5 | Native | *Ipomea pes-capre* subsp. *brasiliensis* L. | 8293 | 20 | 10 |
| | | Exotic | *Ipomea fistulosa* Mart. ex Choisy | 12344 | 20 | 0 |
| Papillionaceae | 6 | Native | *Canavalia cathartica* Thouars | 23393 | 20 | 11 |
| | | Exotic | *Centrosema pubescens* Benth. | 4227 | 20 | 0 |
| Verbenaceae | 7 | Native | *Premna serratifolia* L. | 8775 | 15 | 0 |
| | | Exotic | *Sida acuta* Burm. | 371 | 20 | 0 |
| Malvaceae | 8 | Native | *Thespesia populnea* (L.) Soland. | 18687 | 20 | 10 |
| | | Exotic | *Stachytarpheta urticifolia* Sims | 2117 | 26 | 0 |

matched pairs tests. All tests were performed using Statistica 5.1 (Statsoft Inc. 1998).

## Results and discussion

Our results support the anecdotal evidence that *A. dispersus* prefer exotic hosts; significantly greater numbers of egg spirals ($n = 8$, $Z = 2.38$, $P < 0.02$, Fig. 1) and pupae ($n = 8$, $Z = 1.96$, $P < 0.05$, Fig. 2) were found on exotic than native hosts. Contrary to our expectations this pattern is not explained by differences in biotic resistance between plant groups. The biotic resistance hypothesis, posits that less species rich communities will be easier to invade because the likelihood of encountering a competitor or a fortuitously pre-adapted predator, parasite or pathogen is lower (Elton 1958; Levine et al. 2004). In this study the mean numbers of putative species recorded per leaf did not differ between exotic and native plants ($n = 8$, $Z = 0.85$, $P = 0.4$). Likewise there were no differences between recorded herbivore ($n = 8$, $Z = 0.28$, $P = 0.78$, Fig. 3) and *A. dispersus* predator densities ($n = 8$, $Z = 0.70$, $P = 0.48$, Fig. 4). These results suggest that biotic resistance due to competition for feeding sites or enemy free space has not strongly affected *A. dispersus* population growth in Seychelles.

Most studies of biotic resistance have focused on plant invasions. These show that native generalist herbivores tend to suppress populations of invasive plants (for meta-analyses see Levine et al. 2004; Parker et al. 2006). Comparatively few studies provide evidence of biotic resistance at higher trophic levels (Baltz and Moyle 1993; Harvey et al. 2004; De Rivera et al. 2005; Kushner and Hovel 2006). In this study we did not detect the predicted differences in community structure between native and exotic plants that would have implied a role for biotic resistance. For logistical reasons we focused only on arthropods present on leaves during day light hours for the duration of the study period. In consequence we may have inadvertently ignored many arthropods from other feeding guilds. Given the importance of interactions between above and below ground

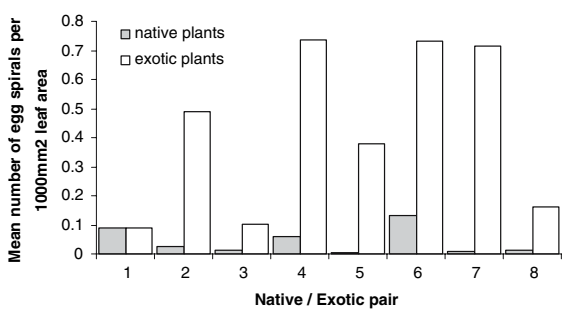



**Fig. 1** Mean numbers of *A. dispersus* egg spirals per 1,000 mm$^2$ of leaf area for each native/exotic plant pair (see Table 1)

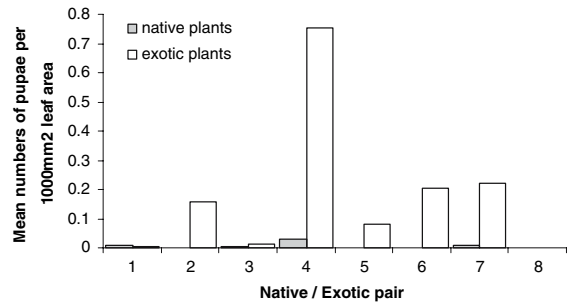



**Fig. 2** Mean numbers of *A. dispersus* pupae per 1,000 mm$^2$ of leaf area for each native/exotic plant pair (see Table 1)

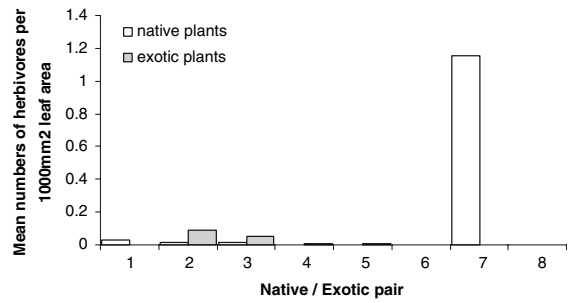



**Fig. 3** Mean numbers of herbivores per 1,000 mm$^2$ of leaf area for each native/exotic plant pair (see Table 1)

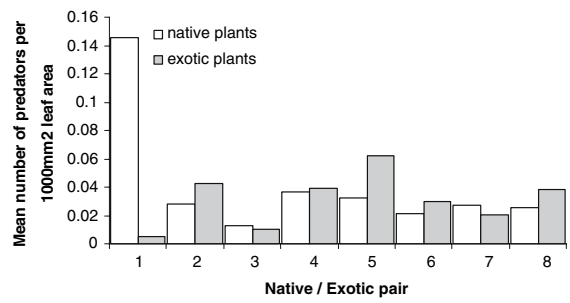



**Fig. 4** Mean numbers of putative predators per 1,000 mm$^2$ of leaf area for each native/exotic plant pair (see Table 1)

competitors (Soler et al. 2005) and the potential for interactions between both spatially (Bezemer et al. 2005; Bezemer and van Dam 2005; van Ruijven et al. 2005) and temporally (Ohgushi 2005) separated organisms, a far more detailed study would be required to categorically rule out biotic resistance.

Additional whitefly abundance data were collected on Cousin Island, an island nature reserve that was formerly a coconut plantation but has been carefully restored by the removal and management of invasive plants since 1968. Comparison of the Mahé and Cousin data shows that plants on Mahé hosted significantly more egg spirals ($n = 8$, $Z = 2.52$, $P = 0.01$; Fig. 5) and pupae ($n = 8$, $Z = 2.03$, $P = 0.04$; Fig. 6) than plants on Cousin Island. Although our data provide a very weak test (one between island comparison only) this result suggests that the abundant exotic host plants on Mahé have facilitated the invasion of *A. dispersus* in Seychelles. Recent work on old-field grassland in the Northern Great Plains of North America shows that ecological restoration using native species can limit the spread of invasive grasses (Bakker and Wilson 2004). Furthermore, work by Scoppettone et al. (2005) indicates that the restoration of Mojave Desert oasis spring systems may encourage re-colonisation by native fish and protect against further invasions. Our data suggest that habitat degradation on Mahé may be an important factor in determining the current abundance and distribution of *A. dispersus* in Seychelles but that habitat restoration could provide a sustainable, long-term management solution in some areas.

Many alternative 'invasion success' hypotheses focus on positive interactions between invaders (Simberloff and Von Holle 1999). Successful

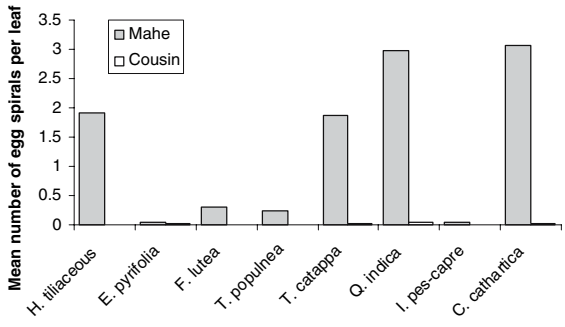



**Fig. 5** Mean numbers of *A. dispersus* egg spirals per leaf for plants found on both Mahé and Cousin Island

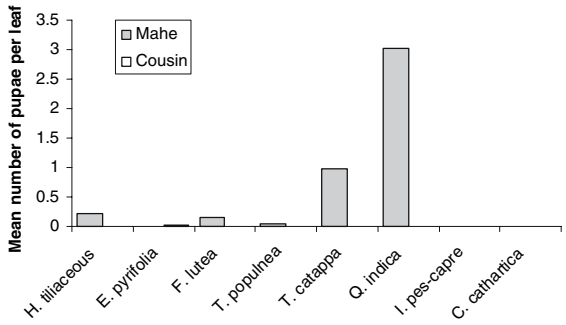



**Fig. 6** Mean numbers of *A. dispersus* pupae per leaf for plants found on both Mahé and Cousin Island

invasions often involve suites of organisms that share a home range and are therefore also likely to have a shared evolutionary history (Crosby 1986; Simberloff and Von Holle 1999). In this study an equal number of exotic plant species (*C. pubescens* and *I. fistulosa*) and native plant species (*T. catappa* and *I. pes capre*) originate from or are widely distributed in Central America and the Caribbean (the native range of *A. dispersus*); most of the remaining plants are of Asian or African origin (Robertson 1989). In contrast, *Aleurodicus dispersus*, which was unknown to science until it began to spread rapidly around the tropics in the 1960's, is rare within its native range (Russell 1965; Kumashiro et al. 1983). Furthermore, *A. dispersus* rarely kill their hosts even at high densities (Kumashiro et al. 1983), although losses in terms of yield in agricultural crops often range from 50% to 80% in any one season (Wen et al. 1995; Geetha 2000). Thus it seems unlikely that most *A. dispersus* hosts would have experienced selection strong enough to cause the population level differentiation in resistance or tolerance required to produce the kind of pattern found here.

In order to gain a better understanding of the factors that promote the establishment of *A. dispersus* in the absence of its natural enemies we tested *A. dispersus* abundance on native versus exotic hosts, the potential for biotic resistance on native versus exotic plants, and establishment of *A. dispersus* on an island with numerous exotic plants versus establishment on an island with very few exotic plants. Our results show that exotic host plants are preferred over native host plants. Contrary to our expectations this pattern was not explained by a failure of biotic resistance due to enemy release on exotic plants.

Densities of *A. dispersus* were found to be significantly lower on host plants on Cousin Island, where invasive plants are removed and the ecosystem has been restored, than on Mahé. These observations indicate that the success of *A. dispersus* may not be exclusively due to the absence of its natural enemies. Indeed the success of *A. dispersus* appears to be linked to the spread of exotic host plants. Consequently, we argue that invasive species management schemes on small Oceanic islands should focus on habitat restoration where appropriate. This strategy has obvious conservation benefits and may also provide longer lasting and more robust protection against invasion than comparatively short term and considerably more risky biological control strategies (Louda et al. 2003).

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