

Saving a tropical ecosystem from a destructive ant-scale (*Pheidole megacephala*, *Pulvinaria urbicola*) mutualism with support from a diverse natural enemy assemblage

R. Gaigher · M. J. Samways · S. Van Noort

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Abstract Ants can disrupt the natural biological control of serious hemipteran pests by interfering with natural enemies, resulting in a change in ecosystem functioning. We focus here on interference by a highly invasive ant *Pheidole megacephala* on the regulation of a tree destroying hemipteran scale insect *Pulvinaria urbicola* on Cousine Island in the Seychelles archipelago, a tropical island ecosystem. We show how a diverse natural enemy assemblage contributes substantially to the collapse of the ant-scale mutualism following managed ant suppression. Natural enemy abundance and species richness increased significantly after ant suppression, with varying responses among the different functional guilds. Primary parasitoids coexisted with tending ants before ant suppression, but could not regulate the enormously high scale densities alone. After ant suppression, a significant increase in predators caused a collapse of the scale population. Guilds external to the mutualism were also affected, with primary parasitoids of various non-hemipteran taxa also increasing, which contributed significantly to

the recovery of the community to its pre-invasion composition. Our results highlight the far-reaching and pervasive effects of the hemipteran-tending invasive ant within the natural enemy assemblage. In turn, we also illustrate the potential to restore the tropical ecosystem by encouraging an array of natural enemies through precision management of the ant.

Keywords Parasitoids · Predators · Invasive species · Island restoration · *Pheidole megacephala* · *Pulvinaria urbicola*

Introduction

Ants and honeydew-producing hemipteran insects are commonly associated through trophobiotic mutualisms, where hemipterans provide ants with food in return for tending services and protection from natural enemies (Delabie 2001). Natural enemy exclusion, harassment and mortality by tending ants can interfere significantly with the biological control of hemipteran populations (Eubanks et al. 2002; Kaplan and Eubanks 2002; Mgocheki and Addison 2009) and can have important consequences for both plant protection and conservation (Styrsky and Eubanks 2007).

Research on the disruption of biocontrol by ants has typically focused on interactions between the ant, hemipteran pest and pertinent natural enemy species (Cardinale et al. 2003; James et al. 1999; Letourneau

R. Gaigher (✉) · M. J. Samways
Department of Conservation Ecology and Entomology,
and DST/NRF Centre of Excellence for Invasion Biology,
Stellenbosch University, Private Bag X1, Matieland 7602,
South Africa
e-mail: reneg@sun.ac.za

S. Van Noort
Natural History Department, Iziko South African
Museum, PO Box 61, Cape Town 8000, South Africa

and Andow 1999). However, most biological control systems involve diverse assemblages of natural enemies (Snyder and Ives 2003) and there is increasing evidence for the effect of the mutualism on the broader natural enemy community. Recent studies have highlighted the impact of honeydew-seeking ants on suites of beneficial arthropods (Eubanks et al. 2002; Kaplan and Eubanks 2002; James et al. 1999; Kaplan and Eubanks 2005) and have demonstrated the variable responses of different natural enemies to ant aggression (Daane et al. 2007; Völkl 1992; Völkl and Mackauer 1993). There has also been focus on interactions among natural enemies in relation to ant tending and its consequences for pest regulation (Kaneko 2003; Kaneko 2007; Liere and Perfecto 2008). These mutualisms are clearly enmeshed in complex, interconnected assemblages and the dynamics within these interaction webs can be variable, with important implications for pest management in both agricultural and natural systems.

Here we adopt a community approach to assess the pest regulation of an exotic scale insect, *Pulvinaria urbicola* (Homoptera: Coccidae), within a complex natural ecosystem. The study was conducted on Cousine Island, a small island in the Seychelles that has undergone conservation restoration. The scale insect occurred in extremely high densities in parts of the native forest, facilitated greatly by its mutualism with the invasive ant *Pheidole megacephala*, and was responsible for damage to native trees throughout the high density area (Gaigher et al. 2011). Biological control of *P. urbicola* can be achieved by various natural enemy species including the parasitoid wasps *Coccophagus ceroplastae*, *Euryischomyia flavithorax* and *Metaphycus luteolus*, the coccinellid *Cryptolaemus montrouzieri* and scale pathogen *Verticillium lecanii* (Smith et al. 2004). But, it is often released from natural enemies in its introduced range, and in association with aggressive, effective mutualist partners like *P. megacephala*, it can reach outbreak densities (Gaigher et al. 2011; Handler et al. 2007; O'Neill et al. 1997).

In response to concerns about the impact of the mutualism on the native forest, a management program was initiated consisting of a toxic ant baiting campaign (Gaigher et al. 2012) which resulted in disruption of the mutualism and a significant decline in scale insect density shortly after ant control (Gaigher and Samways 2013). This study documents the

concurrent response of the natural enemy assemblage to the decoupling of the mutualism. The aim is to (1) assess the effect of ant interference with scale biocontrol by examining the mechanisms responsible for the scale decline after ant suppression, and (2) to investigate the interactions of the mutualists within the broader natural enemy assemblage.

Methods

Study design

Cousine Island is a 27 ha granitic island in the Seychelles archipelago at 4°20'41"S and 55°38'44"E. *P. megacephala* and its mutualistic soft scale *P. urbicola* occurred at low densities throughout most of the island, but at very high densities in a continuous 8 ha area in the northern parts of the island. The ants were suppressed to insignificant levels in this area through toxic baiting in May 2010 (methods described in Gaigher et al. 2012), which resulted in decoupling of the mutualism and a significant decline in scale insect density (Gaigher and Samways 2013).

Forty permanent monitoring sites were selected on the island, 20 of which were within the 8-ha baited area and 20 were outside the baited area. The limitation of this design is that the samples are not from independent treatments (Hulbert 1984), as there was only one baited area. This is a common caveat of invasion studies where the invasion itself is not replicated (Hoffmann 2010; Krushelnycky and Gillespie 2008). We aimed to account for the lack of independence by sampling throughout the greatest possible extent of the baited and unbaited areas, with maximum distance between monitoring sites.

At each site, estimates of natural enemy abundances were made 2 weeks before baiting, 2 weeks after baiting, 1 month after baiting, 4 months after baiting, and 11 months after baiting. Natural enemies were monitored at each survey time using one 8 × 20 cm yellow sticky trap hung in the lower canopy at each monitoring site. Traps were collected after 3 days. For less mobile species, the lower tree canopies in a 10 × 10 m area were inspected for 5 min per site per survey, and all predators and parasitoids were recorded. Species that could not be identified in the field were collected with an aspirator

Table 1 Natural enemies recorded during the survey on Cousine Island May 2010–May 2011

Family	Species	Guild	Host/prey
<i>Parasitoids</i>			
Aphelinidae	<i>Coccophagus</i> sp. 1	Prim	Hemiptera
	<i>Marietta leopardina</i> *	Sec	Hemiptera
Bethyidae	Genus A sp. 1	Prim	Various taxa
	Genus B sp. 1	Prim	Various taxa
	Genus C sp. 1	Prim	Coleoptera
Braconidae	<i>Chelonus</i> sp. 1	Prim	Lepidoptera
	Genus A sp. 1	Prim	Lepidoptera
	Genus B sp. 1	Prim	Various taxa
Ceraphronidae	<i>Ceraphron</i> sp. 1 & 2	Sec	Various taxa
Chalcididae	<i>Brachymeria</i> sp. 1	Prim or Sec	Various taxa
	<i>Brachymeria</i> sp. 2	Prim or Sec	Various taxa
	<i>Hockeria</i> sp. 1	Prim	Lepidoptera
Encyrtidae	<i>Anicetus</i> sp. 1*	Prim	Hemiptera
	<i>Aphycus</i> sp. 1*	Prim	Hemiptera
	<i>Cheiloneurus cyanonotus</i> *	Sec	Hemiptera
	<i>Cheiloneurus</i> sp. 2	Sec	Hemiptera
	Genus A sp. 1	Prim or Sec	Various taxa
Eulophidae	<i>Homalolytus</i> sp. 1	Prim	Coleoptera
	<i>Metaphycus</i> sp. 1*	Prim	Hemiptera
	<i>Aprostocetus</i> sp. 1*	Prim	Hemiptera
Eupelmidae	<i>Pediobius</i> sp. 1	Prim	Various taxa
	<i>Sympiesis</i> sp. 1	Prim	Various taxa
Eupelmidae	<i>Eupelmus</i> sp. 1	Prim or Sec	Various taxa
Figitidae	<i>Ganaspis</i> sp. 1 & 2	Prim	Diptera
Mymaridae	<i>Gonatocerus</i> sp. 1	Prim	Hemiptera
Platygastridae	<i>Gryon</i> sp. 1	Prim	Various taxa
	<i>Gryon</i> sp. 2	Prim	Various taxa
	<i>Palpoteleia</i> sp. 1	Prim	Various taxa
	<i>Synopeas</i> sp. 1	Prim	Diptera
	<i>Synopeas</i> sp. 2	Prim	Diptera
Pteromalidae	<i>Moranila</i> sp. 1	Prim	Hemiptera
	<i>Spalangia</i> sp. 1	Prim	Diptera
	<i>Spalangia</i> sp. 2	Prim	Diptera
	<i>Sycoscapter</i> sp. 1	Prim	Hymenoptera
<i>Beetles</i>			
Coccinellidae	<i>Chilocorus nigrinus</i>	Pred	Hemiptera

Table 1 continued

Family	Species	Guild	Host/prey
	<i>Cryptolaemus montrouzeiri</i>	Pred	Hemiptera
	<i>Phlyctenolotis scotti</i>	Pred	Various taxa
	<i>Stethorus</i> cf. <i>aethiops</i>	Pred	Various taxa
	<i>Sticholotis madagassa</i>	Pred	Hemiptera
<i>Spiders</i>			
Araneidae	<i>Neoscona subfusca</i>	Pred	Various taxa
Salticidae	<i>Heliophanus</i> sp. 1	Pred	Various taxa
	<i>Heliophanus</i> sp. 2	Pred	Various taxa
	<i>Myrmarachne constricta</i>	Pred	Various taxa
Theridiidae	<i>Theridion</i> sp. 1	Pred	Various taxa
Uloboridae	<i>Uloborus</i> sp. 1	Pred	Various taxa
	<i>Undetermined</i> sp. 1	Pred	Various taxa

Species with asterisks were also reared from the dominant scale insect *Pulvinaria urbicola*. Guild abbreviations Prim Primary parasitoid, Sec secondary parasitoid, Prim or sec primary or secondary parasitoid, Pred predator

and identified in the laboratory. Data from yellow sticky traps and direct surveys were combined.

To supplement our data on parasitoids, we collected parasitized scales opportunistically throughout the survey period. Scales were placed in rearing boxes (10 × 10 × 15 cm) and adult parasitoids were collected as soon as they emerged into the attached test tubes (50 ml, 2.5 cm diameter).

Specimens were identified to the lowest taxonomic level possible. Species that could be assigned with certainty to functional guilds based on their level of identification were grouped appropriately into primary parasitoids, secondary parasitoids and predators, and were further assigned to groups based on their hosts or prey (Table 1). A few parasitoids could be identified only to family level and were assigned to a separate primary or secondary parasitoid group, as their exact functional guild was uncertain. This group was excluded from analyses assessing guild responses. Parasitoid specimens were deposited in the Iziko South African Museum, predatory beetles in the Stellenbosch University Entomological Museum and spiders in the South African Arachnid Collection.

Data analyses

To determine whether there was a significant response in (1) overall natural enemy abundance and species richness, and (2) abundance of the different functional guilds to the disruption of the mutualism, Generalized Estimating Equations (GEEs) were done in SPSS 19 (SPSS Inc. 2010). GEE's extend the generalized linear model algorithm to account for correlated repeated measurements (Liang and Zeger 1986), and also adjust for overdispersion (Stokes et al. 2000). 'Plot' was specified as the subject variable in the model, and 'time' and 'treatment' as within-subject variables, with the important term in the analysis being the 'time by treatment' interaction, which indicates whether there is change over time as a result of treatment. This analysis examines the relative change in baited and unbaited areas, and thus accounts for external ecological influences that are unrelated to baiting on response variables. A Poisson distribution and log link function was specified for all models (McCullagh and Nelder 1989). Bootstrap pairwise comparisons were performed to account for non-normal response.

Non-metric multivariate analyses were done in Primer 5.2.9 (Clarke and Gorley 2001) so as to investigate the effect of mutualism disruption on the natural enemy assemblage structure. Data were pooled for each treatment (baited or unbaited) per time, and a similarity matrix was constructed using the Bray-Curtis similarity measure based on $\log(x + 1)$ transformed abundance data. Patterns in natural enemy assemblages among groupings were then graphically represented using non-metric multidimensional scaling (nMDS) ordination plots (Clarke and Warwick 2001).

To test for significant differences in natural enemy assemblages among groupings, one-way analyses of similarities (ANOSIM) were performed, and similarity percentage analyses (SIMPER) were performed to detect the species that contributed most to differences between groupings of interest. The ratio of the average dissimilarity among groupings (Dis) and the associated standard deviation (SD) indicates how consistently a species contributes to differences between groupings. Species with a high Dis/SD ratio are considered to be key discriminating species (Clarke and Warwick 2001) and therefore species with a ratio

>1 were analysed further. Relative abundances for each of the discriminating species were displayed by superimposing bubble plots on the nMDS ordination plot to indicate the relative contribution of those species to ordination patterns.

Results

Forty-six natural enemy species in 40 genera and 17 families were recorded during the survey (Table 1). Thirty-four of these species were parasitoid wasps and included 26 primary parasitoid species, four secondary parasitoid species and four primary or secondary parasitoids. 12 predator species were recorded. Within these groups, almost a third of all species parasitize or prey on hemipterans, whereas the others specialize on various non-hemipteran taxa or are generalist natural enemies (Table 1). An additional six species that occurred as singletons were recorded, but were excluded from analyses and further discussion to focus on responses of great biological significance. Parasitoid species that were also reared from scales included *Metaphycus* sp. 1, *Aprostocetus* sp. 1, *Anicetus* sp. 1, *Aphycus* sp. 1, *Cheiloneurus cyanonotus* and *Marietta leopardina* (Table 1). The first four species are primary scale parasitoids and the last two are secondary parasitoids.

There was a significant response in natural enemy abundance (Wald Chi square = 11.97, $P = 0.02$) and species richness (Wald Chi square = 46.52, $P < 0.0001$) to the disruption of the mutualism (Fig. 1, Table 2). In baited areas, overall abundance increased significantly after baiting and then decreased to pre-baiting levels at the end of the survey 11 months after baiting, with two peaks in abundance at 2 weeks and 4 months after baiting. Natural enemy species richness increased steadily to 4 months after baiting in baited areas and then declined to pre-baiting levels 11 months after baiting (Fig. 1). There was fluctuation in abundance and richness in unbaited areas, but much less pronounced than in baited areas, with both showing a maximum at 4 months after baiting (Fig. 1).

Primary parasitoid abundance showed a significant response to baiting (Wald Chi square = 19.54, $P = 0.001$), including groups with hemipteran (Wald Chi square = 55.12, $P < 0.0001$), and non-hemipteran hosts (Wald Chi square = 38.13, $P < 0.0001$)

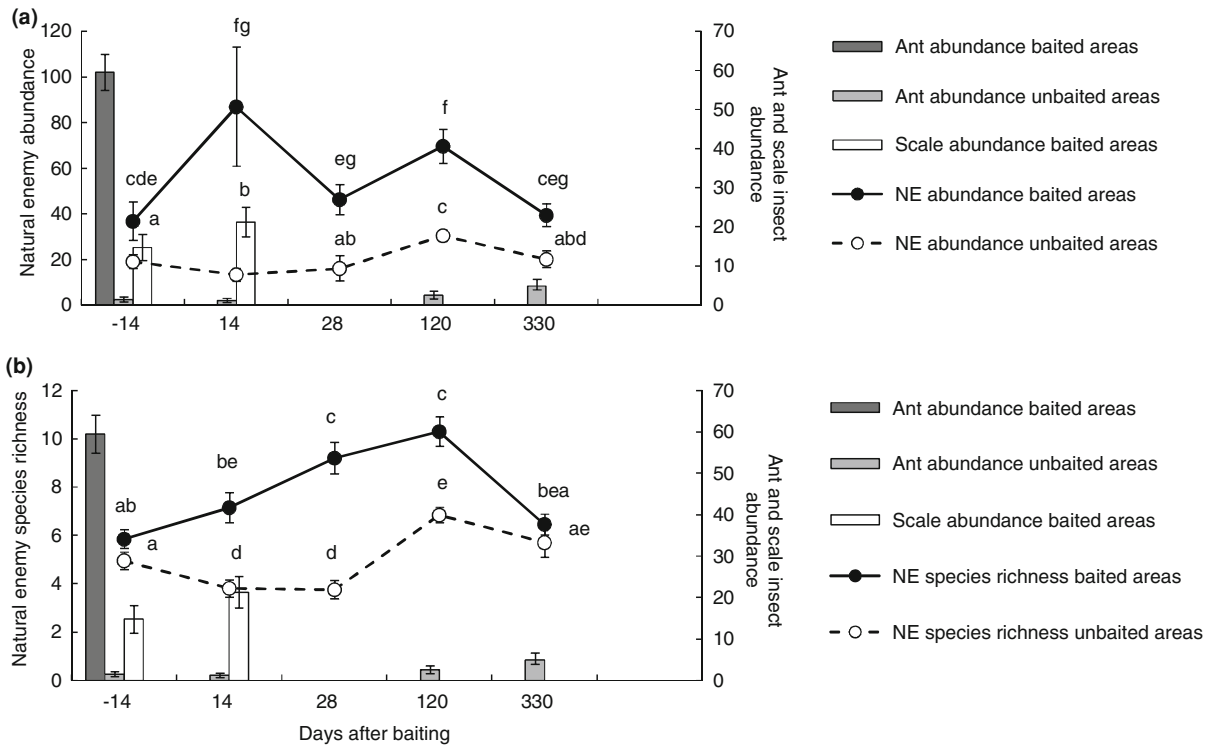


Fig. 1 Natural enemy (NE) **a** abundance and **b** species richness, as well as ant and scale abundance (\pm SE) in baited and unbaited areas before and after mutualism disruption. Treatment date is indicated by the arrow. Natural enemy means

with letters in common are not significantly different at $P < 0.05$. Ant and scale data were obtained from Gaigher et al. (2012). Ant and scale abundance was not assessed at 28 days after baiting

Table 2 The effect of mutualism disruption on the overall natural enemy abundance and species richness

Response variables	df	Wald's Chi square	<i>P</i>
<i>Natural enemy abundance</i>			
Treatment	1	32.61	<0.0001
Time	4	31.05	<0.0001
Time x Treatment	4	11.97	0.02
<i>Natural enemy species richness</i>			
Treatment	1	43.78	<0.0001
Time	4	77.07	<0.0001
Time x Treatment	4	46.52	<0.0001

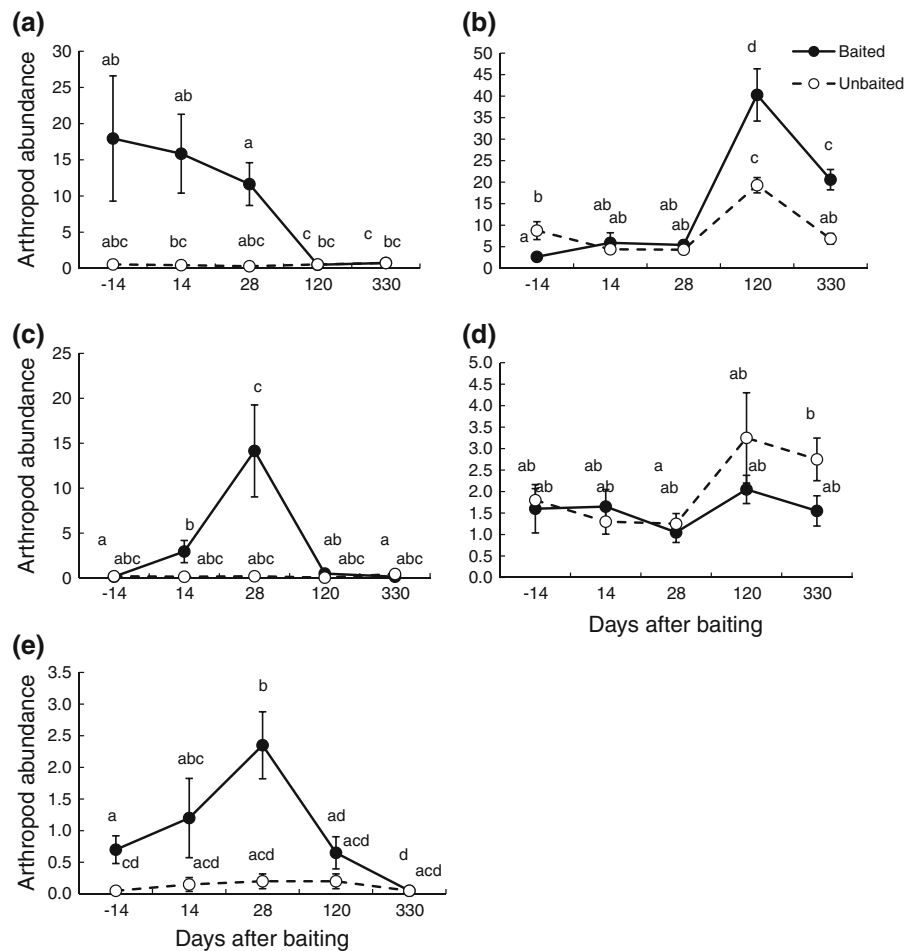
Statistics derived from generalized estimating equations

(Fig. 2a–b, Table 3). Primary parasitoids with hemipteran hosts were highest pre-baiting and declined to low levels 4 months after baiting (Fig. 2a), whereas those with non-hemipteran hosts increased after baiting and showed a peak in abundance at 4 months after baiting (Fig. 2b). Overall predator abundance

was significantly influenced by baiting (Wald Chi square = 88.85, $P < 0.001$). Predators specializing on Hemiptera showed a significant response (Wald Chi square = 38.62, $P < 0.0001$), but not generalist predators (Wald Chi square = 5.66, $P = 0.23$) (Fig. 2c–d, Table 3). Predators with hemipteran prey increased after baiting with maximum abundance 1 month after baiting, and declined to pre-baiting levels at the end of the survey (Fig. 2c). Generalist predator abundance fluctuated in both treatments (Fig. 2d). Response in secondary parasitoids was non-significant (Wald Chi square = 4.05, $P = 0.40$), but abundance was significantly higher in baited areas one month after baiting (Fig. 2e).

Natural enemy assemblage structure differed significantly among treatments and times (Global $R = 0.48$, $P < 0.001$; Fig. 3, Table 4). Baited areas early in the survey (BT1–BT3) were different from all other groupings (R range = 0.45–0.90; Fig. 3, Table 4), whereas baited areas later in the survey (BT4 and BT5) resembled unbaited areas more closely

Fig. 2 The abundance of different functional guilds before and after mutualism disruption in baited and unbaited areas: **a** primary parasitoids with hemipteran hosts **b** primary parasitoids with various hosts, **c** predators with hemipteran prey, **d** generalist predators and **e** secondary parasitoids. Means with letters in common are not significantly different at $P < 0.05$. Groups not shown did not have sufficient data at all survey periods to carry out the analyses



(R range = 0.18–0.74) than early baited areas (R range = 0.62–0.90).

We report SIMPER results only for species discriminating between BT1 and UT1 to highlight differences between baited and unbaited areas pre-baiting, and between BTU1 and BTU5 to highlight how the baited areas changed over time. Key discriminating species between BT1 and UT1 were Encyrtidae Genus B sp.1, *Aphycus* sp. 1, *Palpoteleia* sp. 1, *Spalangia* sp. 1 and *Phlyctenolotis scotti* (Fig. 4, Table 5). All except for *P. scotti* also accounted for most of the differences between BT1 and BT5, and also included *Synopeas* sp. 1 (Fig. 4, Table 5). Encyrtidae Genus B sp. 1 and *Aphycus* sp. 1 (usually associated with Hemiptera) were most abundant in the early baited plots (BT1-3) whereas the other four species (parasitoids and predator of various taxa) increased in later baited areas (BT4-5).

Discussion

Mechanism of hemipteran decline

Management of the mutualism was effective due to the presence of a remarkable abundance of natural enemies on the island. After the tending ants were suppressed, there was a great increase in natural enemy abundance and richness that corresponded with the rapid, area-wide decline of the scale population. These results are consistent with other studies that have shown that ant suppression can enhance the biological control of hemipterans (Daane et al. 2007; Del-Claro and Oliveira 2000; Queiroz and Oliveira 2001; Renault et al. 2005; Vanek and Potter 2010).

It is unlikely that all of the natural enemies were involved in scale regulation, but for many we are certain of their role in *P. urbicola* control. Six of the 34

Table 3 The effect of mutualism disruption on abundance of natural enemy feeding guilds

Response variables	df	Wald's Chi square	P
<i>Overall primary parasitoids</i>			
Treatment	1	40.92	<0.0001
Time	4	282.00	<0.0001
Time x Treatment	4	19.54	0.001
<i>Primary parasitoids with hemipteran hosts</i>			
Treatment	1	56.33	<0.0001
Time	4	33.08	<0.0001
Time x Treatment	4	55.12	<0.0001
<i>Primary parasitoids with various taxa as hosts</i>			
Treatment	1	2.75	0.98
Time	4	217.64	<0.0001
Time x Treatment	4	38.13	<0.0001
<i>Overall predators</i>			
Treatment	1	8.04	0.005
Time	4	20.58	<0.0001
Time x Treatment	4	88.85	<0.001
<i>Predators with hemipteran prey</i>			
Treatment	1	12.86	<0.001
Time	4	37.01	<0.0001
Time x Treatment	4	38.62	<0.0001
<i>Predators with various taxa as prey</i>			
Treatment	1	2.05	0.15
Time	4	23.86	<0.0001
Time x Treatment	4	5.66	0.23
<i>Overall secondary parasitoids</i>			
Treatment	1	10.37	0.001
Time	4	29.86	<0.0001
Time x Treatment	4	4.05	0.40

Groups not listed did not have sufficient data at all survey periods to carry out the analyses. Statistics derived from generalized estimating equations

parasitoid species recorded are primary scale parasitoids (Noyes 2012; Scholtz and Holm 2008). Of these, the genera *Moranila*, *Coccophagus*, *Anicetus*, *Aphycus* and *Metaphycus* all include economically important species that have been introduced for control of agricultural soft scale pests (Myers et al. 1989). *Anicetus* sp. 1, *Aphycus* sp. 1 and *Metaphycus* sp. 1, as well as *Aprostocetus* sp. 1 were also reared from *P. urbicola* in this study. Additionally, scale insects are the main prey for three of the 12 predators recorded; *Chilocorus nigritus*, *Cryptolaemus montrouzieri* and

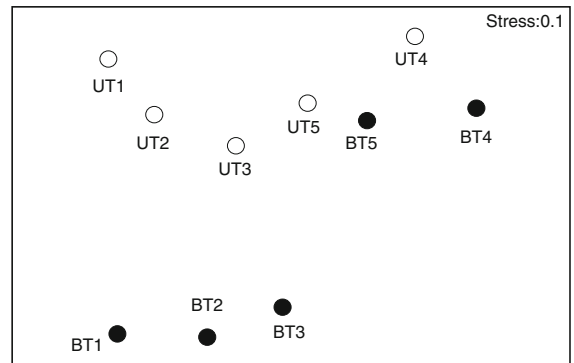


Fig. 3 nMDS ordination plot of time and treatment groupings (UT1-UT5 = unbaited plots, time 1-5; BT1-BT5 = baited plots, time 1-5) based on $\log(x + 1)$ transformed abundance data

Sticholotis madagassa. All three coccinellids are voracious scale and mealybug predators that are widely used in biocontrol programs (Jalali and Singh 1989; Kaur and Vink 2012; Samways and Wilson 1988). These results suggest that the interference of the ants with the top-down control of the herbivore pest was strong and pervasive, and enabled the scale to reach damaging levels, even in the presence of a diverse natural enemy assemblage.

Ant interference with natural enemies is well documented (Renault et al. 2005; Majerus et al. 2006; Suzuki and Ide 2008). However, ant attendance can have varying effects on different natural enemies (Daane et al. 2007; Völkl and Mackauer 1993) and may also mediate interactions among them (Kaneko 2007; Kaneko 2002), making the effects of ant suppression unpredictable. This is apparent from the diverse responses of the different guilds involved with the mutualism on the island. Primary parasitoids of hemipterans were at their highest abundance before baiting despite high ant densities, and declined after baiting, whereas predators of hemipterans increased to their highest abundances 1 month after ant suppression.

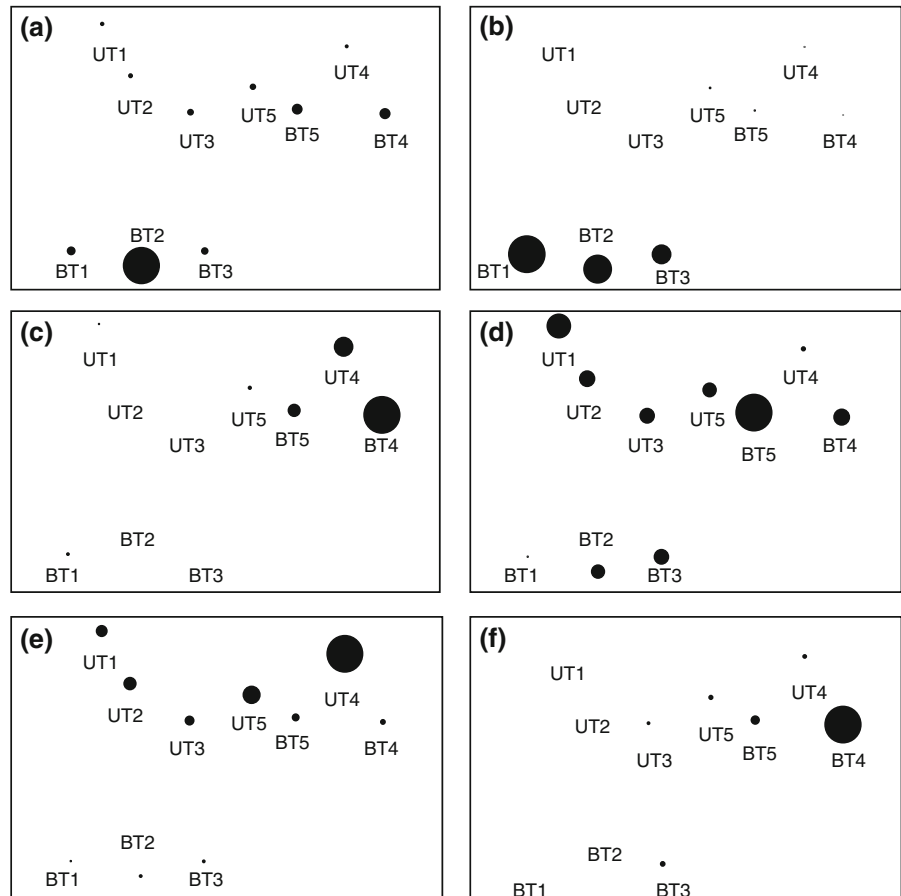
Many parasitoids have adaptations that allow them to persist in the presence of ants (Daane et al. 2007; Bartlett 1961), including species in some of the genera recorded here e.g. *Coccophagus* sp. (Bartlett 1961) and *Metaphycus* sp. (Barzman and Daane 2001). These species often select ant-tended hemipteran colonies that provide them with enemy-free space where they are protected from intraguild predation and hyperparasitism (Völkl 1992; Barzman and Daane 2001). Pre-baiting ant attendance seemed to promote high primary parasitoid densities in this way. Yet

Table 4 R-statistics derived from ANOSIM indicating similarities in natural enemy assemblage structure among baited and unbaited areas at different times after baiting (BT1-BT5 = baited plots, time 1–5, UT1-UT5 = unbaited plots, time 1–5)

	BT1	BT2	BT3	BT4	BT5	UT1	UT2	UT3	UT4	UT5
BT2	0.19									
BT3	0.46	0.26								
BT4	0.81	0.83	0.90							
BT5	0.62	0.67	0.81	0.48						
UT1	0.57	0.57	0.65	0.68	0.44					
UT2	0.63	0.52	0.60	0.74	0.51	0.02				
UT3	0.61	0.48	0.52	0.64	0.41	0.08	-0.04			
UT4	0.65	0.84	0.91	0.64	0.40	0.63	0.71	0.64		
UT5	0.35	0.45	0.57	0.20	0.18	0.22	0.27	0.20	0.34	

Values closer to 0 indicate greater similarity and values closer to 1 indicate greater differences. The low significance level was due to Bonferroni correction for multiple comparisons

Fig. 4 Abundances of key discriminating species
a Encyrtidae genus B sp. 1,
b *Aphycus* sp. 1, **c** *Spalangia* sp. 1, **d** *Palpoteleia* sp. 1,
e *Phlyctenolotis scotti*,
f *Synopeas* sp. 1, accounting for most of the variation between baited and unbaited groupings, as well as pre- and post-baited groupings, superimposed onto the nMDS ordination of the groupings. Bubble size represents abundance. (BT1-BT5 = baited plots, time 1–5, UT1-UT5 = unbaited plots, time 1–5)



clearly, this guild alone was not effective at reducing high scale densities.

The scale population collapsed with the increase in hemipteran-feeding predators 1 month after baiting.

Other multi-taxa studies have indicated that increased predator diversity can enhance pest suppression (Cardinale et al. 2003; Colfer and Rosenheim 2001; Costamagna et al. 2008). But predator identity also

Table 5 Results from SIMPER analyses showing relative mean abundances of key discriminating species (as indicated by Dis/SD > 1) and their contributions to dissimilarities

between pre-baiting baited and unbaited sites (BT1 and UT1) and baited sites at the start and end of the survey (BT1 and BT5)

	Mean abundance		Dis/SD	% Contribution to dissimilarity	Cumulative % dissimilarity
	BT1	UT1			
Average dissimilarity = 79.19 %					
<i>Encyrtidae</i> Genus B sp. 1	12.65	5.35	1.44	15.86	15.86
<i>Aphycus</i> sp. 1	16.2	0.2	1.27	14.76	30.62
<i>Palpoteleia</i> sp. 1	0.3	6	1.49	13.95	44.57
<i>Spalangia</i> sp. 1	2.15	0.95	1.12	7.8	52.36
<i>Phlyctenolotis scotti</i>	0.1	0.8	1.03	4.68	63.14
Average dissimilarity = 62.4 %					
	BT1	BT5			
<i>Palpoteleia</i> sp. 1	0.3	9.2	2.34	17.55	17.55
<i>Spalangia</i> sp. 1	2.15	9.85	1.67	13.81	31.37
<i>Aphycus</i> sp. 1	16.2	0.55	1.2	13.37	44.74
<i>Encyrtidae</i> Genus B sp. 1	12.65	15.75	1.17	9.41	54.15
<i>Synopeas</i> sp. 1	0	0.9	1.25	5.01	59.16

seems to be a key determinant of the outcome, as the occurrence of species with high per capita feeding rates can have disproportionately large effects on pest control within multi-taxa systems (Chalcraft and Reseterits 2003; Denoth et al. 2002; Straub and Snyder 2006). Our findings are consistent with these ideas. 96 % of the scale predator abundance here was *C. nigritus*, a species with a very high feeding rate that was successfully introduced to the Seychelles for biocontrol of scale on coconut palm (Samways and Wilson 1988). This species operates well in combination with parasitoids, as it suppresses hemipterans that escape parasitism at high densities, but is less effective when prey is scarce (Samways 1984, 1988). Primary parasitoids declined with the declining scale population, but remained in the area at low densities, suggesting that there was potential for an additive effect of the predators and parasitoids on pest suppression in the absence of the ants.

Interactions with the broader natural enemy assemblage

The natural enemy assemblage as a whole showed a significant response to mutualism disruption. Assemblages in the baited areas changed over time to resemble those in the unbaited areas towards the end of the survey, suggesting a return to an assemblage structure more similar to pre-invasion conditions.

Both the guild and assemblage analyses indicated that mutualism disruption influenced not only natural enemies involved in the mutualism, but also affected groups external to the mutualism.

Primary parasitoids with various taxa as hosts increased in abundance over time, and four of the key discriminating species between invaded and uninvaded areas were species that parasitize or prey on various non-hemipteran taxa. Previous studies on this system indicated that the abundance of many soil-surface and canopy arthropods increased after the baiting program (Gaigher et al. 2012; Gaigher and Samways 2013), and it is likely that the increase in these natural enemies was in response to the recovery of potential hosts and prey. These results support the argument that ant tending of hemipterans can have far-reaching effects in ecosystems (Styrsky and Eubanks 2007; Grover et al. 2008), as the effects of the mutualism carried across trophic levels, influencing various guilds within this functionally important assemblage.

Conservation implications

The great variety of natural enemies is noteworthy considering the island's small size and the isolation of the Seychelles archipelago. Other islands with similar environmental conditions and pest species have required introductions of biocontrol agents in conjunction with ant control to reduce *P. urbicola*

densities (Smith et al. 2004; Smith and Papacek 2002). The persistence of natural enemies in the environment can increase the options for managing hemipteran pests, and is promising for future pest management in the Seychelles. Cousine supports five other scale species in addition to the dominant *P. urbicola* (Gaigher and Samways unpublished data), and many of these species and other coccids have been implicated in damage to native trees on other Seychelles islands (Haines and Haines 1978; Hill et al. 2003; Hill and Newbery 1982). It is encouraging that with targeted and careful management of the highly destructive ant-hemipteran mutualism, this complex of natural enemies can be re-established to continue to maintain the scale at a low population level where natural ecosystems are no longer seeing a major ecological regime shift.

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