LETTER

Invasional 'meltdown' on an oceanic island

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Abstract

Islands can serve as model systems for understanding how biological invasions affect community structure and ecosystem function. Here we show invasion by the alien crazy ant *Anoplolepis gracilipes* causes a rapid, catastrophic shift in the rain forest ecosystem of a tropical oceanic island, affecting at least three trophic levels. In invaded areas, crazy ants extirpate the red land crab, the dominant endemic consumer on the forest floor. In doing so, crazy ants indirectly release seedling recruitment, enhance species richness of seedlings, and slow litter breakdown. In the forest canopy, new associations between this invasive ant and honeydew-secreting scale insects accelerate and diversify impacts. Sustained high densities of foraging ants on canopy trees result in high population densities of host-generalist scale insects and growth of sooty moulds, leading to canopy dieback and even deaths of canopy trees. The indirect fallout from the displacement of a native 'keystone' species by an ant invader, itself abetted by introduced/cryptogenic mutualists, produces synergism in impacts to precipitate invasional 'meltdown' in this system.

INTRODUCTION

Rapid state changes in ecosystems (Scheffer *et al.* 2001) caused by invasive alien species may be particularly apparent on oceanic islands where native biotas are disharmonic (Carlquist 1965), functional redundancy low (Denslow 2003), food webs simple (Pimm 1991), and the fractions of introduced species large (Vitousek *et al.* 1996). Social insects, especially ants, are one of the most devastating groups of invaders (Moller 1996; Chapman & Bourke 2001; Holway *et al.* 2002). Most analyses focus on the direct effects of invasive alien ants, primarily on assemblages of native ants and other arthropods (e.g. Holway 1999; Le Breton *et al.* 2003; Sanders *et al.* 2003), although a few studies have explored indirect effects, mainly on plants (e.g. Bond & Slingsby 1984; Carney *et al.* 2003). Broader impacts, especially in natural ecosystems, are poorly explored and understood.

In this study, we examined direct and indirect impacts of the yellow crazy ant *Anoplolepis gracilipes*, one of the most widespread, abundant, and damaging of invasive ants (Holway *et al.* 2002). It has invaded continents and islands across the Tropics (Haines *et al.* 1994), including Christmas Island, a 134-km² high island in the northeastern Indian Ocean. In island rain forest this omnivorous ant forms expansive and polygynous (multiple-queened) supercolonies

in which workers occur at extremely high densities (1000s ants/m²). This 'tramp' ant reached the island over 70 years ago, and for decades persisted at extremely low population densities, which had no obvious impact on the island's native biota. First detected in 1989, supercolonies have become progressively more widespread since the mid-1990s; by 2001, crazy ant supercolonies covered *c.* 25 km², about one-quarter of all island rain forest. We compare sites recently invaded by *A. gracilipes* to intact control sites to infer impacts and quantify state shifts caused by this invasive alien species in a natural ecosystem.

METHODS

All sampling was conducted in the dry season (September–December in 1998 and 1999) in rain forest on Christmas Island (10°29′S, 105°38′E), an isolated oceanic island in the northeastern Indian Ocean. The island is mostly covered by rain forest, described in detail elsewhere (Mitchell 1975). Supercolonies of *A. gracilipes*, typically with sharply defined boundaries (10s of metres), created a mosaic of invaded and uninvaded rain forest across the island. We located six 1 ha sites haphazardly in invaded forest and paired each of these with a 1 ha uninvaded site of similar structure. Paired sites (blocks) were always positioned within 200 m of each other,

and blocks were separated by 1–9 km across the island. We have been visiting these areas regularly since 1989, and crazy ants spread to all invaded sites only 1–2 years prior to this study.

We haphazardly set out five 4 m × 4 m plots at each site; in total, we sampled 80 m^2 each in invaded and control plots in each of six areas (60 plots, a total of 960 m^2). Activity of *A. gracilipes* was calculated as the total number of ants recovered from a single 5 cm × 5 cm absorbent pad soaked in a 30% v/v sucrose solution placed on the ground in the centre of the plot, divided by time (15–20 min) the bait was exposed. For impacts, we counted the number of dead land crabs and the number of crab burrows, and we estimated percentage litter cover using a point intercept method (the presence/absence of leaf litter was assessed at each of 49 intersections on a string grid 50 cm × 50 cm). Further, we identified and counted by species every seedling <200 cm in height on each plot.

For canopy impacts, we determined ant densities on tree boles, scale insect abundance and sooty mould cover on leaves and stems and canopy condition, for each of five canopy trees (>20 cm DBH) at each site. Ant densities on canopy tree boles were determined by applying a 16.5 cm wide strip of sticky cloth tape around one-half of the bole of each tree at breast height, and then counting and identifying captured ants. We used a slingshot and line to pull down a large branch from each tree canopy, from which five shoots were haphazardly selected. Scale insects were counted under magnification (10–15X) on a randomly chosen 20 cm section of each shoot, and on a randomly chosen, fully expanded leaf from each shoot. Sooty mould cover on these stems and leaves was rated as 0–20 (0), 21–40 (1), 41–60 (2), 61–80 (3), or 81–100 (4) percentage cover. Canopy condition was assessed by collecting 30 shoots from each branch and determining the proportion of shoots with new leaf growth. Seasonally deciduous tree species were not included in estimates of canopy condition.

For each variable, values were pooled or averaged over all quadrats or trees sampled at each site to produce a site value ($n = 6$ each for invaded and uninvaded sites). Data were analysed using a randomized-block ANOVA, where site pairs were blocks; block effects were not significant ($P > 0.05$) for all variables. Residuals were inspected and data transformed as necessary to improve homogeneity of variances. We used Non-metric Multidimensional Scaling (NMDS, using the Bray-Curtis dissimilarity coefficient) followed by ANOSIM (analysis of similarities) on log ($x + 1$)-transformed data to compare relative species abundance of seedlings on ant-invaded and uninvaded sites (Clarke & Warwick 1994). ANOSIM is a non-parametric permutation procedure that tests hypotheses about sample (site) similarity.

Canopy tree species composition at each site was characterized by selecting and identifying 50 trees >20 cm

DBH in a random walk (Greig-Smith 1983). Presence or absence of canopy dieback in each tree was determined with binoculars. Hierarchical, log-linear modeling (Tabachnick & Fidell 1996) was used to test whether the proportion of trees that showed evidence of dieback differed between ant-invaded and uninvaded sites. Relative to most continental tropical rain forests, forest diversity on Christmas Island is low: observed richness ranged from 8 to 15 species in 50-tree samples per site. Using the Michaelis–Menten estimator to predict species richness asymptotes (Colwell 2002), most tree species richness (74–84%) was captured in these samples, based on 50 randomizations for each site.

RESULTS

Anoplolepis gracilipes was abundant at invaded sites, but rare to absent in intact control sites (Table 1a). In fact, activity of *A. gracilipes* at sugar baits was more than 100-fold greater in invaded sites, where they foraged continuously on the forest floor and canopy. Red land crabs were abundant in intact forest, but were rare to absent at sites invaded by *A. gracilipes* (Table 1b); the average density of red crab burrows exceeded 1 m^{-2} at intact sites, but was only 0.03 m^{-2} in invaded sites, a 42-fold difference. This dramatic difference was reflected in crab mortality; dead crabs were abundant at invaded sites, but absent at intact control sites.

Litter and seedling recruitment dynamics were significantly altered in the near-absence of red crabs (Fig. 1). On average, litter cover was double, seedling density was 30-fold higher, and seedling species richness was 3.5-fold higher in ant-invaded areas (Table 1c,d). The relative species composition of seedlings in the understorey differed significantly between invaded and intact sites (Fig. 2a; stress = 0.11, ANOSIM $P = 0.009$), whereas we found no relationship between canopy tree composition and the invasion status of sites (Fig. 2b; stress = 0.12, ANOSIM $P = 0.835$).

High densities of crazy ants streamed up and down the boles of canopy trees at invaded sites, whereas ants were rarely found on trees at uninvaded sites (Table 1e). The gasters of most foraging ants returning to the forest floor were expanded and translucent, indicating that they had been collecting honeydew in the canopy. These high densities of crazy ants on trees in invaded areas coincided with significantly larger populations of scale insects and the spread of honeydew-dependent sooty moulds over most canopy stems and leaves (Table 1f–g). Population outbreaks of the cryptogenic lac insect *Tachardina aurantiaca* (Kerridae) and introduced *Coccus celatus* (Coccidae), in particular, were associated with sites invaded by *A. gracilipes*. These host-plant generalists are, respectively, associated with at least 21 and 10 tree species on the island, including most canopy dominants.

Variable	Invaded (mean ± 1 SE)	Uninvaded (mean ± 1 SE)	$F_{1,5}$	P-value
Forest floor				
(a) *Anoplolepis* activity index*	6.96 (1.42)	0.06 (0.06)	45.40	0.001
(b) Land crabs				
Crab burrows/80 m^2	2.3 (1.6)	95.7 (24.5)	44.82	0.001
Dead crabs/80 m^2	51.8 (17.5)	0.0 (–)	18.81	0.007
(c) Litter cover (%)	87 (3)	43 (13)	21.43	0.006
(d) Seedlings				
Number of seedlings/80 m^2	1375.8 (166.2)	44.7 (16.7)	123.59	<0.001
Number of spp./80 m^2	22.2 (2.6)	6.3 (1.3)	34.06	0.002
Forest canopy				
(e) *Anoplolepis*/100 cm^2 bole	4.5 (0.4)	0.3 (0.1)	137.65	<0.001
(f) Scale insects				
Stem (no./20 cm)	114.7 (35.6)	8.2 (4.9)	17.85	0.008
Leaf (no./leaf)	122.5 (45.0)	7.1 (3.0)	59.29	0.001
(g) Sooty mould rating†				
Stem	2.2 (0.4)	0.4 (0.2)	43.39	0.001
Leaf	2.0 (0.6)	0.2 (0.1)	26.11	0.004
(h) Percentage growing shoots	72.7 (8.9)	96.0 (0.9)	10.14	0.024

Table 1 Impacts on the forest floor and in the canopy following alien ant invasion. F and P are statistics derived from separate randomized block ANOVAs for each variable; all block effects were not significant ($P > 0.05$)

*Ants per sugar bait divided by minutes bait exposed.

†Qualitative index of percentage cover on stems and leaves.

These positive, population-level consequences of the association between *A. gracilipes*, scale insects, and sooty moulds help explain the lower proportion of growing shoots on canopy trees at ant-invaded sites (Table 1h) and the higher frequency of tree dieback. Tree dieback depended on ant invasion [at invaded sites, 51% of trees (146/286) showed evidence of dieback; at uninvaded sites just 18% of trees were affected (53/294), $\chi^2 = 77.7$, $P \ll 0.0001$, log-linear analysis].

Dieback effects were differential and influenced both seedling and canopy species composition. Both seedlings and trees of *Inocarpus fagifer*, a nitrogen-fixer and forest dominant, were heavily infested and especially affected by lac scale insects in areas of *Anoplolepis* invasion: *Inocarpus* comprised 24% of all seedlings we censused on uninvaded plots, but we encountered only 10 *Inocarpus* seedlings (0.1% of all seedlings) on *Anoplolepis*-invaded plots. Deaths of *Inocarpus* trees also occurred disproportionately in ant-invaded sites. At two invaded sites where we counted dead standing canopy trees, *Inocarpus* comprised 83% (15/18) and all (6/6) dead trees whereas they comprised only 28% (28/100) and 22% (22/100) of live canopy trees sampled at random at the respective sites ($\chi^2 = 17.85$, $P < 0.001$, chi-square test, and $\chi^2 = 17.71$, $P < 0.001$, Fisher exact test).

DISCUSSION

A common characteristic of islands is the relative simplicity of their biotic communities, providing tractable systems for

analyses of biological invasions (Vitousek 2002). Changes in the abundance of species affect the structure and functioning of ecosystems (Chapin *et al.* 1997), and both retrospective reconstruction of impacts (Fritts & Rodda 1998) and experimental additions of invaders (Schoener & Spiller 1999) illustrate that single consumer species can have wide-ranging direct and indirect effects on island communities. These effects are especially evident on Christmas Island because the dominant native omnivore, the red land crab, is deleted by the ant invader. In the absence of ant invasion, these crabs are abundant, occurring at densities of up to 1.8 m^{-2} and 1500 kg ha^{-1} (Green 1997).

The direct impact of this introduced ant on the dominant endemic consumer has long-term implications for forest structure and composition through indirect effects on seedlings and changes in habitat structure. Previous observations and experiments conducted at a small spatial scale (25 m^2) have shown that removal of red crabs deregulates seedling recruitment, seedling species composition, litter breakdown, and the density of litter invertebrates (O'Dowd & Lake 1989, 1990; Green *et al.* 1997, 1999). Elimination of this key native consumer by a single species of invasive ant recapitulates these effects, but at a landscape scale. For seedlings, invasion by crazy ants indirectly acts as a 'diversity enhancer' (Schoener & Spiller 1996), but is likely to reduce directly species richness of the litter and canopy fauna. Red crabs also provide 'biotic resistance' to invaders, including some introduced plant

Figure 1 Impacts of invasion of island rain forest by the yellow crazy ant, *Anoplolepis gracilipes*. (a) Uninvaded site (Winifred Track) with open understorey maintained largely by the foraging activities of the red land crab, *Gecarcoidea natalis*. (b) Invaded site (Dales) 1–2 years after ant invasion with a dense and diverse seedling cover and thick litter layer. Photographs by Peter Green.

and mollusc species (O'Dowd & Lake 1990; Lake & O'Dowd 1991), and we predict accelerated rates of secondary invasion following their deletion from ant-invaded rain forest.

It has been estimated that 10-15 million red crabs, or one-quarter to one-third of the entire population, have been killed by this invasive ant over the last several years across *c.* 25 km^2 of rain forest (P. Green, unpubl. data). Crazy ants kill red crabs through sheer force of numbers and constant activity, overwhelming the crabs by spraying formic acid over their eyes and mouthparts. Although the exact physiological mechanism by which formic acid kills crabs is unknown, death is usually swift and occurs within 48 h. As supercolonies spread, crazy ants occupy red crab burrows, kill and consume resident crabs, and use burrows as nest sites. Furthermore, large numbers of red crabs are killed in transit during their annual migration (Hicks 1985), when migratory pathways intercept *Anoplolepis* supercolonies. This effect at a distance can deplete crab populations in areas not directly invaded by the crazy ant, setting in train indirect effects on seedling abundance and litter decomposition. However, this was unlikely to have affected control plots during our study; burrow densities on these plots were within the range reported prior to the widespread formation of crazy ant supercolonies (Green 1997).

Mutualism plays an important but underappreciated role in the successful invasion by alien species, and can amplify and diversify their impacts (Simberloff & Von Holle 1999; Richardson *et al.* 2000). This may be especially so for *A. gracilipes* and other invasive tramp ants which form close mutualistic relationships with honeydew-secreting Homoptera (Van der Goot 1916; Helms & Vinson 2002). On
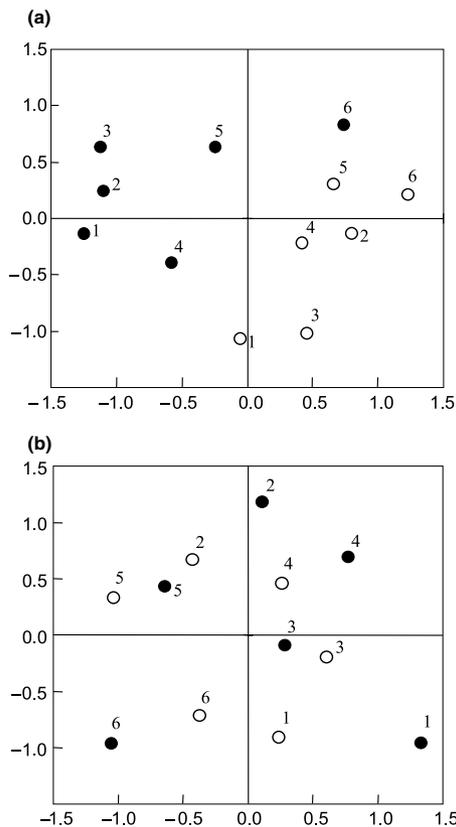
Figure 2 Non-metric multidimensional scaling of relative species composition of (a) seedlings and (b) canopy trees at rain forest sites either invaded (solid circles) or uninvaded (open circles) by the yellow crazy ant *Anoplolepis gracilipes*. For seedlings, stress = 0.11, analysis of similarities, *P* = 0.009. For canopy trees, stress = 0.12, ANOSIM, *P* = 0.835. Numbers refer to paired invaded and uninvaded sites: 1, Dolly Beach; 2, Dales; 3, Greta Beach; 4, Winifred Track; 5, Hidden Valley, and 6, Tate Point.

Christmas Island, outbreak densities of scale insects associated with *Anoplolepis* supercolonies appear to cause dieback in the canopies of large trees (cf. Bach 1991), and may further impair tree performance through the deposition of excess honeydew on their leaf surfaces. Honeydew encourages the development of sooty moulds (Capnodiaceae), which reduce photosynthesis (Wood *et al.* 1988). Ant-scale associations are often adventive and generalized, and need not be generated by a coevolutionary history (Simberloff & Von Holle 1999). Invasive impacts may depend upon serial introductions of different scale insect species capable of establishing mutualism with *Anoplolepis*. Positive population-level consequences magnify impacts of both.

Our results show that reconfiguration of species interactions following the deletion of a dominant native omnivore by an alien invasive omnivore unleashes both 'bottom up' and 'top down' effects that are rapidly transforming this island rain forest ecosystem. These multitrophic-level distortions are comparable in scope to those witnessed following deletion of top consumers from tropical rain forest on man-made islands (Terborgh *et al.* 2001). Furthermore, positive interactions between this dominant, invasive ant and other introduced species amplify and diversify impacts. Changes in the web of interactions following multiple alien species introductions can lead to synergism in invasive impact to precipitate invasional 'meltdown' (Parker *et al.* 1999; Simberloff & Von Holle 1999).

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