Invasive ants disrupt frugivory by endemic island birds

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Biological invasions can alter direct and indirect interactions between species, generating far-reaching changes in ecological networks that affect key ecological functions. We used model and real fruit assays to show that the invasion and formation of high-density supercolonies by the yellow crazy ant (YCA), *Anoplolepis gracilipes*, disrupt frugivory by endemic birds on Christmas Island, Indian Ocean. The overall handling rates of model fruits by birds were 2.2–2.4-fold lower in ant-invaded than in uninvaded rainforest, and pecking rates by two bird species declined by 2.6- and 4.5-fold, respectively. YCAs directly interfered with frugivory; their experimental exclusion from fruiting displays increased fruit handling threefold to sixfold, compounding indirect effects of ant invasion on resources and habitat structure that influence bird abundances and behaviours. This invasive ant, whose high densities are sustained through mutualism with introduced scale insects, rapidly decreases fruit handling by endemic island birds and may erode a key ecological function, seed dispersal. Because most other invasive ant species form expansive, high-density supercolonies that depend in part on association with hemipteran mutualists, the effects that we report here on avian frugivore–plant associations may emerge across their introduced ranges.

Keywords: biological invasions; islands; mutualism; plant–animal interactions; seed dispersal

1. INTRODUCTION

Biological invaders can reconfigure species interactions to disrupt, replace or facilitate native plant–animal mutualisms (Traveset & Richardson 2006; Foster & Robinson 2007). Ants are increasingly moved by humans across biogeographic barriers (Suarez *et al.* 2005) and some have established around the globe, producing major ecological consequences for recipient communities (Lach & Hooper-Bui 2009). Most attention has focused on impacts of invasive ants on native ants, but adverse effects extend to many organisms, including birds (Lach & Hooper-Bui 2009).

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One widespread plant–animal mutualism is between fleshy-fruited plants and birds (Dew & Boubli 2005). Fruit is a primary resource for many birds and provides a key ecological function, seed dispersal, for much of the world's flora (Sekercioglu 2006). We investigated whether ant invasion disrupts frugivory by comparing fruit handling by two endemic birds, the Island thrush (*Turdus poliocephalus erythropleurus*) and the Christmas Island (CI) white-eye (*Zosterops natalis*), in forest invaded or uninvaded by *Anoplolepis gracilipes*, the yellow crazy ant (YCA). YCA has invaded pantropically (Wetterer 2005) and, like many invasive ants (Tsutsui & Suarez 2003), forms expansive supercolonies with high, sustained densities of workers. On CI (Indian Ocean), supercolonies have spread to over 30 per cent of the rainforest, where they affect the abundance, behaviour and reproductive success of forest birds (Davis *et al.* 2008).

2. MATERIAL AND METHODS

The study was conducted in the understorey of primary rainforest on CI (10°25' S, 105°40' E) during the transition from dry to wet season (October–January). CI is oceanic (135 km², maximum elevation 360 m) and dominated by a broad-leaved, structurally simple tropical rainforest. Many woody plants have fleshy fruits or arillate seeds (44%, *n* = 108 species) and the fruit/aril colours of species in the forest understorey are red–orange (50%), black (25%), white (10%), pink (10%) or yellow (5%), and diaspore diameters averaged 5.5 mm (range 2–15 mm, *n* = 20; P. T. Green 1994–2009, unpublished data).

High-density supercolonies of the YCA were always associated with highly elevated densities of exotic, honeydew-secreting scale insects (especially *Tachardina aurantiaca* (Kerriidae) and *Coccus celatus* (Coccidae), both broad host–plant generalists; O'Dowd *et al.* 2003). YCA invasion has generated a mosaic of three forest states, primarily by extirpating a keystone native consumer (the red land crab, *Gecarcoidea natalis*) (Green *et al.* 2008). We chose five 1 ha sites of each state (i.e. YCA-invaded sites, where supercolonies had formed 1.5–2 years prior to the study; intact sites where supercolonies had never formed; and ghosted sites, which had not been invaded but where resident red crabs had been depopulated when previous crab breeding migrations intercepted supercolonies and were killed) to estimate the effects of ant invasion on avian frugivory. Sites were interspersed (0.7–10.7 km apart) across the island and spread across similar elevations (Davis *et al.* 2008). The inclusion of ghosted sites allowed a comparison of impacts in the absence of both the native red crab and YCAs to those in the absence of crabs only, and in the presence of both species. This helped distinguish direct effects of ants on fruit handling from their indirect effects on resource levels and habitat structure.

Artificial fruiting displays and model fruits were used to measure fruit handling by birds (figure 1*a,b*). Displays were wooden dowels (0.8 cm diameter × 45 cm length), each with five holes 4 cm apart through which galvanized wire (0.7 mm diameter) was threaded. Model fruits (12 mm diameter) were moulded from non-toxic, odourless and water-resistant red Plastalina modelling clay and pressed onto the outer, up-facing ends of wires (10 fruits per display). Ten displays were attached to separate understorey plants at breast height and placed greater than 25 m apart within a 100 m × 50 m plot. One fruit survey was completed at each site in October, November and January. Each survey was over 4 days at five sites, staggered randomly within each month. Artificial displays allow standardization of the number and arrangement of fruits and placement within sites. The colour and size of model fruits can be controlled, as they neither rot nor desiccate, and records of visitation are retained. The number and type of peck marks could be assigned to the thrush (figure 1*c*) and white-eye (figure 1*d*) because of different bill morphologies and gape widths (thrush: 13.97 ± 0.52 mm, *n* = 3; white-eye: 6.47 ± 0.03 mm, *n* = 3). The diameter of model fruits was large relative to the gape widths of these two frugivorous birds to minimize chances of fruit removal and hence retain feeding attempts.

We compared the handling of model fruits to real fruits of *Schefflera elliptica* (Araliaceae) at a different ant-invaded site. Ripe fruits were orange–red and 5.1 mm in diameter (*n* = 100).

Figure 1. (a) Artificial fruiting display with model fruits, (b) red model fruits (scale bar, 1 mm) handled by the thrush ((c) left fruit; credit: Kee Seng Foo) or white-eye ((d) right fruit; credit: Tony Patisser).

The presentation of displays was as for the fruit handling survey, except that 20 displays each of real and model fruits were used. We excluded ants from 10 displays of each by placing Tanglefoot bands at the base of each dowel. YCA numbers on each display were recorded after 2 days. After 4 days, handling rates were determined.

Bayesian analyses were used throughout (see the electronic supplementary material). The total number of fruits that had peck marks and the total number of peck marks made by each bird species per site were examined for variation among forest states using Bayesian analysis of covariance. For comparison of the handling rates of real and model fruits, and for the test for direct interference by ants on fruit handling, we analysed probabilities that fruits in a display would be handled, numbers of ants per display and peck marks per display of model fruits.

3. RESULTS

Average handling rates depended on forest state (figure 2a; electronic supplementary material, table S1). Of the 1151 model fruits that were handled (26% of all fruits presented), the handling rates were 2.2 and 2.4 times lower in ant-invaded sites than in intact and ghosted sites, respectively. Handling differences between uninvaded intact and ghosted sites were indistinguishable. Consumptive attempts by the two birds mirrored those for total fruit handling (figure 2b,c). The thrush contributed 32 per cent of total peck marks while the white-eye made 68 per cent ($n = 1750$). Pecking rates were 2.6 and 4.5 times lower for the thrush and 2.6 and 3.5 times lower for the white-eye in ant-invaded sites than in intact and

ghosted sites, respectively. For the white-eye, pecking rates were similar between uninvaded intact and ghosted sites (figure 2b), but pecking by the thrush was 40 per cent greater in ghosted than in intact sites (figure 2c). Thrush and white-eye peck marks were positively and negatively related to understorey vegetation density, respectively (see electronic supplementary material, table S1).

The numbers of model and real fruits handled by birds were 6.4 and 3.5 times higher, respectively, on ant-excluded displays than on displays accessible to YCAs (figure 2d). The probability that fruits in a display would be handled by birds did not differ between model and real fruits ($S_2 = 0.059 \pm 0.247$ s.d., odds ratio (OR) = 2; see electronic supplementary material for definitions) and ant exclusion greatly increased the probability that a display would be visited ($T_2 = 2.018 \pm 0.286$, OR = ∞) (figure 2e). Fewer ants occurred on displays with real fruits than on those with model fruits ($S_2 = -0.548 \pm 0.206$, OR = 499) and much fewer on ant-excluded displays than on ant-accessible displays ($T_2 = -1.580 \pm 0.264$, OR = ∞) (figure 2e). Peck marks were six times more frequent on displays of model fruits from which ants had been excluded (8.9 ± 2.9 versus 1.4 ± 0.6 on ant-exclusion displays versus ant-access displays, respectively; $T_2 = 1.875 \pm 0.289$, OR = ∞).

Figure 2. (a) Number of model fruits handled per site by birds (mean + 1 s.e.), and total pecks per site by (b) the thrush and (c) white-eye in the three forest states ($n = 5$ sites each). Bars with different letters differ significantly (see electronic supplementary material, table S1). (d) Number of model fruits (mean + s.e., open bars) and fruits of *S. elliptica* (shaded bars) pecked by birds per display and (e) number of YCAs (mean + s.e.) on displays either accessible to or excluded from ants at an ant-invaded site. $n = 10$ displays per treatment.

4. DISCUSSION

Evidence was compelling that the thrush and white-eye were less likely to handle model fruits in forests with YCA supercolonies. Birds handled *S. elliptica* and model fruits at similar rates, increasing the confidence that patterns in our experiments reflect natural, expressed differences in frugivory. A reduction in numbers or a redistribution of birds following ant invasion alone does not explain reduced fruit handling by thrushes and white-eyes in ant-invaded sites. Although the abundance of juvenile thrushes was lower in ant-invaded forest, adult thrushes were not and white-eye counts were actually higher (Davis *et al.* 2008). Ant-exclusion experiments showed that the YCA directly interferes with fruit handling by birds. The foraging behaviours and strata use (tree, sapling/shrub or ground layer) of the birds also differ substantially between ant-invaded and uninvaded forest (Davis *et al.* 2008). This broader interference by ants may influence fruit handling by affecting behavioural decisions, including microhabitat selection.

Changes in resource availability and habitat structure following ant invasion should also influence fruit handling. Ant-scale insect mutualism results in a 15-fold increase in scale insects in ant-invaded areas (O'Dowd *et al.* 2003) where scale consumption by the white-eye was 2.5 times greater than in uninvaded forest (Davis *et al.* 2008). If white-eyes focus on this resource in ant-invaded sites, then fruit consumption could decrease, even if white-eye abundance was greater. Fruit handling by white-eyes was similar in the two uninvaded forest states (intact and ghosted). Habitat change was similar in ant-invaded and ghosted forest following loss of land crabs (Davis *et al.* 2008). Thus, the key factor affecting fruit handling rates appears to relate directly to high densities of the YCA in invaded forest rather than to structural changes following elimination of land crabs by YCAs.

Our results have important conservation implications. Invasive ants are well known to disrupt seed removal by native ants (Rowles & O'Dowd 2009). We demonstrated that YCAs can decrease frugivory

by native forest birds. This effect on frugivory emerges just 1–2 years after supercolony formation. High ant densities can be sustained for at least a decade (O'Dowd *et al.* 2003), long relative to the generation times of these birds. The juvenile abundance and nesting success of thrushes are lower in sites with recently formed supercolonies (Davis *et al.* 2008). Hence, if bird populations decline, frugivory may decline in concert with time since invasion. A reduction in fruit consumption in ant-invaded forest over the long term could also affect the local population sizes of birds. Last, ant-imposed reduction of avian frugivory and altered foraging behaviour and microhabitat use by birds are likely to alter seed-dispersal shadows. However, more research is needed because YCAs also extirpate the native red crab, the key post-dispersal seed and seedling predator (Green *et al.* 2008).

Ant invasion foments many changes in this island ecosystem, distorting interactions among trophic levels to affect litter invertebrates, canopy arthropods, phylloplane fungi, seedlings and canopy trees, and understorey birds (O'Dowd *et al.* 2003). It even facilitates secondary invasions, leading to invasional meltdown (O'Dowd & Green 2009). Invader–invader mutualism, involving association between this ant and exotic scale insects (Abbott & Green 2007), sustains high foraging densities of ants sufficient to disrupt native bird–plant associations. Given that a suite of invasive ant species form expansive supercolonies that depend partly on honeydew-secreting Hemiptera (Helms & Vinson 2005; Grover *et al.* 2007), the effects on avian frugivory reported here may be anticipated for other invaded systems.

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