

Invasional meltdown: Invader–invader mutualism facilitates a secondary invasion

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Abstract. In multiply invaded ecosystems, introduced species should interact with each other as well as with native species. Invader–invader interactions may affect the success of further invaders by altering attributes of recipient communities and propagule pressure. The invasional meltdown hypothesis (IMH) posits that positive interactions among invaders initiate positive population-level feedback that intensifies impacts and promotes secondary invasions. IMH remains controversial: few studies show feedback between invaders that amplifies their effects, and none yet demonstrate facilitation of entry and spread of secondary invaders. Our results show that supercolonies of an alien ant, promoted by mutualism with introduced honeydew-secreting scale insects, permitted invasion by an exotic land snail on Christmas Island, Indian Ocean. Modeling of land snail spread over 750 sites across 135 km² over seven years showed that the probability of land snail invasion was facilitated 253-fold in ant supercolonies but impeded in intact forest where predaceous native land crabs remained abundant. Land snail occurrence at neighboring sites, a measure of propagule pressure, also promoted land snail spread. Site comparisons and experiments revealed that ant supercolonies, by killing land crabs but not land snails, disrupted biotic resistance and provided enemy-free space. Predation pressure on land snails was lower (28.6%), survival 115 times longer, and abundance 20-fold greater in supercolonies than in intact forest. Whole-ecosystem suppression of supercolonies reversed the probability of land snail invasion by allowing recolonization of land crabs; land snails were much less likely (0.79%) to invade sites where supercolonies were suppressed than where they remained intact. Our results provide strong empirical evidence for IMH by demonstrating that mutualism between invaders reconfigures key interactions in the recipient community. This facilitates entry of secondary invaders and elevates propagule pressure, propagating their spread at the whole-ecosystem level. We show that identification and management of key facilitative interactions in invaded ecosystems can be used to reverse impacts and restore resistance to further invasions.

Key words: *Anoplolepis gracilipes*; ant–scale insect interactions; biological invasions; biotic resistance; enemy-free space; giant African land snail (*Achatina fulica*); interaction networks; positive interactions; propagule pressure; rain forest (Christmas Island, Indian Ocean).

INTRODUCTION

Human-facilitated movement of species across the globe has been so pervasive that all ecosystems are now multiply invaded (Hobbs et al. 2006). Increasingly, introduced, naturalized species should interact with each other as frequently as with native species. While the direct effect of introduced species on native species has been widely explored (Mack et al. 2000, 2007), invader–invader interactions are likely to have broad, but as yet poorly explored, consequences for invasion success, potentially affecting evolution of species traits, attributes of recipient communities, and propagule pressure.

Mutualism between invaders is posited to initiate invasional meltdown by generating reciprocal, positive population-level responses that amplify invader-specific impacts. These impacts then facilitate further, “secondary” invasions and accelerate the overall rate of invasion (Simberloff and Von Holle 1999). Examples of facilitation of one invader by another are increasingly common (e.g., Adams et al. 2003, Bourgeois et al. 2005, Molina-Montenegro et al. 2008, Best and Arcese 2009, Helms et al. 2011). Nevertheless, invasional meltdown remains controversial because few studies demonstrate positive population-level effects between invaders that amplify their impacts (O’Dowd et al. 2003). Although invader–native interactions can increase abundances of other invaders (Grosholz 2005), no studies yet show that invader–invader interactions facilitate entry and spread of secondary invaders (Gurevitch 2006, Simberloff 2006).

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Here we show that invader–invader mutualism between introduced ants (the yellow crazy ant, *Anoplolepis gracilipes*; “YCA” hereafter) and honeydew-secreting scale insects (*Tachardina aurantiaca* [Kerriidae] and *Coccus* spp. [Coccidae]) facilitates a secondary invasion on an oceanic island. Ant–scale insect association leads to positive population-level feedback resulting in the formation of high-density ant supercolonies that accelerate and diversify impacts across rain forest on Christmas Island, Indian Ocean (O’Dowd et al. 2003, Abbott and Green 2007, Davis et al. 2008, 2010). One key consequence is the rapid reconfiguration of interaction networks in the recipient community. The abundance of a dominant native omnivore–detritivore, the red land crab (*Gecarcoidea natalis*; “RLC” hereafter), is strongly suppressed in YCA supercolonies where ants kill crabs by spraying formic acid in their eyes and mouthparts (O’Dowd et al. 2003). This increases resource levels by deregulating seedling recruitment and leaf-litter breakdown (Green et al. 1997, 1999, 2008). As a predator, the RLC also provides powerful biotic resistance to forest invasion by the giant African land snail (*Achatina (Lissachatina) fulica*; “GALS” hereafter), a renowned pantropical invader. Until recently, GALS never penetrated beyond the disturbed margins of rain forest because they were rapidly discovered and consumed by abundant RLC (Lake and O’Dowd 1991).

The relative importance of invader attributes, traits of the recipient community, and propagule pressure for invasion success, as well as the spatial scale at which these forces act, are poorly understood (Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009). We describe the spatiotemporal pattern of spread of GALS across the island over seven years and use Bayesian hierarchical models to explore whether changes in the recipient community and propagule pressure wrought by invader–invader mutualism influence the probability of invasion by GALS. Incorporation of island-wide management of this exotic ant–scale insect invasion (Abbott and Green 2007, Green and O’Dowd 2009) into the model allowed us to determine whether suppression of ant supercolonies reverses the probability of spread of this introduced land snail. In-site comparisons and experiments were used to determine whether the breakdown of biotic resistance provided by native RLC and creation of enemy-free space by YCA drives the island-wide pattern of land snail invasion.

METHODS

Location and species

Christmas Island (10°25’ S, 105°40’ E) is an isolated oceanic island (135 km², maximum elevation 360 m) in the northeastern Indian Ocean. Over 75% of the island is structurally simple tropical rain forest of relatively low species richness (e.g., 15–20 tree species/ha; Du Puy 1993). Annual rainfall is ~2 m, most of which falls December–May. The red land crab (RLC), an endemic

omnivore, plays a key functional role in the forest understory across the island by largely regulating seedling recruitment and litter breakdown rates (Green et al. 1997, 1999, 2008). The yellow crazy ant (YCA) is a pantropical invader that has spread rapidly across the Indo-Pacific region (Wetterer 2005) and, in association with honeydew-secreting scale insects, can form expansive high-density supercolonies that extend from 1 ha to many square kilometers (Haines and Haines 1978, O’Dowd et al. 2003, Abbott 2005). The giant African land snail (GALS), native to East Africa, has successfully invaded most tropical mainlands and many Indo-Pacific islands (Mead 1979, Raut and Barker 2002). An oviparous hermaphrodite, GALS matures after 5–8 months, can reach 15 cm in length, lays an average of 1000 eggs during its lifetime, can aestivate during dry conditions, and lives up to 5 years (Mead 1961, 1979, Lambert 1974). It has a generalized diet, consuming leaf litter and attacking hundreds of plant species (Raut and Barker 2002). On Christmas Island, GALS was probably introduced during the Second World War as a food source (Sproul 1983).

Island-wide spread of GALS

Spatial and temporal patterns of spread of GALS were determined using presence/absence data collected from a systematic island-wide survey (IWS) repeated biennially, 2001–2007. The IWS was based on a grid of 1024 waypoints (sets of coordinates that identify a point in physical space) spread across the island, including forest and cleared areas on a grid of waypoints at 364-m intervals (Fig. 1). At each waypoint, we also determined YCA activity and RLC burrow density (Green and O’Dowd 2009). Two measures of spread were used: frequency of occurrence of GALS at waypoints and the distance that GALS had invaded from roads and clearings into the forest (90th percentile of distances of waypoints with GALS).

Drivers of GALS spread

We used Bayesian hierarchical modeling of the IWS data (Eq. 1) to calculate the probability of invasion by GALS at a waypoint in one biennial survey (t) as a function of the state of the recipient community at that waypoint, the state of its neighboring waypoints, and of propagule pressure in a previous survey [$(t - 1)$; see Appendix A for full details]. We used only forested waypoints for analyses ($n = 735$ – 740 , depending on survey effort in a given year). The model was

$$\text{logit}(\pi_{j,t}) = a + b_{j(t-1)} + \sum_{i=1}^5 c_i s_{j,i(t-1)} + dg_{j,t-1} + eL_j + u_j;$$

$$O_{j,t} \sim \text{Bernoulli}(\pi_{j,t}); u_j \sim \mathcal{N}(0, \sigma_u);$$

$$\sigma_u \sim \text{Uniform}(0.01, 5); a, b_{2:5}, c_{1:5}, d, e \sim \mathcal{N}(0, 10^4).$$

(1)

The response variable ($O_{i,t}$) was the appearance of land snails between survey t and survey $(t - 1)$, which was compared with sites in which snails had not appeared. Other parameters are defined in the following subsections.

States of recipient communities (b_i)

There were five forest states in the model (Appendix B). *Intact* waypoints (b_1) were those with RLC at very high densities and YCA absent, i.e., the reference condition (term a in the model, Eq. 1). Other terms (b_2 – b_5) were modeled as deviations from this reference condition. *YCA supercolonies* (b_2) were waypoints with YCA present at very high densities, and RLC absent or at very low densities. YCA supercolonies can also indirectly deplete local populations of RLC, by killing en masse migrating crabs that then fail to return to their home areas (O'Dowd et al. 2003, Davis et al. 2008). Thus, *Ghosted* waypoints (b_3) were those with YCA at nil to very low densities, and RLC absent or at very low densities. The final two states result from ongoing management of YCA supercolonies (Green and O'Dowd 2009; Boland et al., *in press*) and allowed us to test for how elimination of YCA supercolonies affected the probability of GALS invasion. Management suppresses high densities of YCA (>99% reduction in worker activity), which can allow for recovery of RLC densities, from no or very little recovery to densities that approximated densities seen at Intact sites. Thus, the final two states were *Baited + high recovery* (b_4 ; YCA supercolonies eliminated with recolonization of RLC to high density) and *Baited + low recovery* (b_5 ; YCA supercolonies eliminated with recolonization of RLC to low density).

States of neighboring communities (c_i)

The third set of terms (c) in the model encapsulates effects on invasion probability of the immediate neighborhood surrounding the recipient community. These estimated whether the proportions of neighbors in any of the five states listed above (c_1 , neighbors Intact; c_2 , neighbors YCA Supercolonies; c_3 , neighbors Ghosted; c_4 , neighbors Baited + high recovery; c_5 , neighbors Baited + low recovery) influenced the probability of invasion by GALS (see Appendix A for full details).

Propagule pressure (d, e)

The other terms (d, e) were factors that could influence propagule pressure. First, we estimated the effect of the proportion of neighbors with GALS on the probability of invasion (d). Second, we included a term (e) that related distance to source areas bordering the forest (cleared areas or major roads) on the probability of GALS invasion (see Appendix A for full details).

In summary, these data track the spread of GALS in space and time at a whole-ecosystem scale. The Bayesian model comprises a whole-island test of the effect of the state of the recipient site, its neighboring sites, and

propagule pressure, both once their original state was altered following YCA invasion (Intact to YCA supercolony or Ghosted states) and then by reversal of those impacts of invasion to allow a return to a condition approaching its original state (YCA suppression and variable recovery of RLC following ant management).

Survival and persistence of GALS

We quantified survivorship of GALS in areas with and without YCA supercolonies and then compared the density and size distribution of GALS at a random set of waypoints either in supercolonies or where supercolonies had never formed. First, we determined experimentally the effect of forest state on GALS survival by translocating 20 tethered adult snails (Lake and O'Dowd 1991) into a 10×10 m quadrat in each of three sites of each forest state (YCA supercolonies, Intact, and Ghosted states), and following their fate daily for the first few days, and progressively less frequently over 180 days. We used an interval-censored Weibull model to analyze differences in GALS survivorship among forest states (see Appendix C for model details).

Second, we considered whether GALS persist once in the forest by comparing their density and size distribution at waypoints with YCA supercolonies ($n = 6$) and those where supercolonies had never formed ($n = 5$) at randomly chosen waypoints in which live GALS were recorded in the most recent IWS (2009). GALS were surveyed along a 50×2 m transect at each site; snails on the ground were surveyed in five quadrats each 4 m^2 at 10-m intervals, while snails on vegetation < 3 m in height were surveyed along the entire transect (see Appendix D for full details). We counted both live snails and empty shells as an integrated measure of both present and past densities. For each site, a composite sample of ground and arboreal snails was generated for analyses of differences in both density and size-class composition. We used the proportion of damaged, broken shells (including live snails and empty shells) as an index of predation pressure, and compared values (GALS density and damage, YCA activity, RLC density) between site types using a two-factor Bayesian model for each variable (see Appendix D for model details).

RESULTS

Island-wide spread of GALS

Giant African land snails (GALS) spread from clearings and increased in frequency across forested waypoints over the island-wide surveys (Fig. 1A). In 2001 they occurred frequently in clearings (20.1% [41/204] of waypoints), but at only 2.5% (18/737) of forested waypoints. Occurrence increased to 2.9% (24/740) of forested waypoints in 2003 and 6.8% (51/738) in 2005. GALS had spread to 10% (72/738) of forested waypoints in 2007. Forest penetration by GALS from edges of clearings increased four-fold, from 189 m in 2001 to 853 m by 2007.

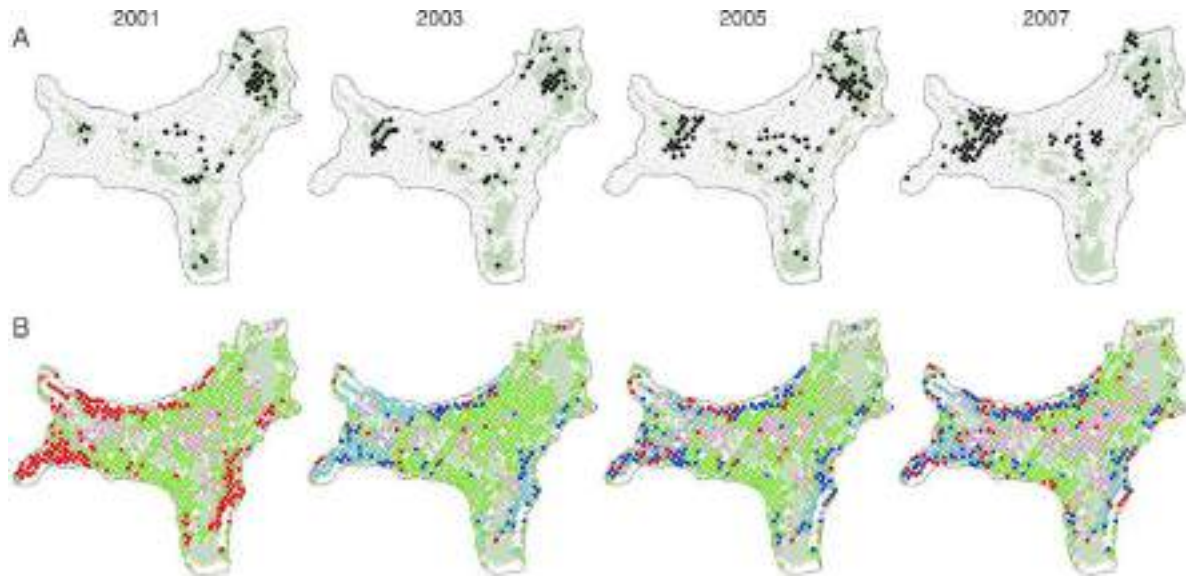


FIG. 1. Spread of the giant African land snail (GALS), *Achatina (Lissachatina) fulica*, and changes in forest state at waypoints in each of four successive island-wide surveys (2001, 2003, 2005, and 2007) on Christmas Island, Indian Ocean. (A) Distribution of GALS occurrences (solid circles). Shaded areas (pale green) are clearings and roads; the small dots depict the grid of waypoints at 364-m intervals. Fewer records in clearings in 2007 were the result of reduced survey effort in clearings that year and not a true reduction in the occurrence of GALS. (B) Distribution of forest states: solid red circles, yellow crazy ant (YCA; *Anaplolepis gracilipes*) supercolonies; dark blue, baited + high recovery of red land crab (RLC; *Gecarcoidea natalis*); pale blue, baited + low recovery of RLC; pink, ghosted waypoints, with YCA and RLC at very low densities; green, intact (see Appendix B for details).

GALS spread into forest amid a shifting mosaic of forest states, a consequence of yellow crazy ant (YCA) invasion and subsequent management to control the ant-scale insect invasion (Fig. 1B; see Methods and Appendix D for forest state definitions). By the initial island-wide survey in 2001, YCA supercolonies had spread to a large fraction of forested waypoints (24%, 175/737) and occupied ~2500 ha. Over all surveys, YCA supercolonies had directly or indirectly affected nearly three quarters of all forested waypoints (71.7%, ~7200 ha); supercolonies were recorded at 33.1% of waypoints while a further 38.6% of waypoints were ghosted in at least one survey. The proportion of waypoints with supercolonies declined precipitously following widespread aerial baiting in 2002 (to <100 ha) and remained relatively low with continuing ground-based baiting (3% [23/741] in 2003, 6% [43/738] in 2005, and 10% [73/737] in 2007) (Fig. 1B). Red land crabs (RLC) then began recolonizing former YCA supercolonies. By 2007, 57% (98/189) of baited waypoints had recovered densities of RLC comparable to Intact sites (>0.2 burrows/m²). Intact waypoints decreased by nearly one third over time, from 53% in 2001 to 38% in 2007, mostly as new supercolonies developed, but also as ghosting increased (from 23% of waypoints in 2001 to 27% in 2007) (Fig. 1B). GALS spread was most rapid in the west of the island in an area surrounded by YCA supercolonies in 2001 and in the central region where waypoints with Ghosted forest increased (Fig. 1B).

Drivers of GALS spread

The status of the recipient community had a very important effect on the probability of invasion by GALS (*a* and *b* parameters in Table 1; Fig. 2). From 2001 to 2007, the probability of GALS occurrence at Intact sites with abundant RLC was very low (probability of GALS invasion, $P = 0.002$) but was 14-fold higher for Ghosted sites ($P = 0.028$), and 253-fold greater for sites with YCA supercolonies ($P = 0.506$) (Table 1). Whole-island management of YCA supercolonies using aerial baiting reversed the probability of GALS invasion at baited sites where RLC numbers recovered; these sites (Baited + high recovery) did not deviate from the reference condition (Intact; OR = 1.7 [where OR = odds ratio; i.e., the ratio of posterior odds to prior odds]) and had a near-identical probability of GALS invasion ($P = 0.004$ vs. $P = 0.002$). Further, GALS were much less likely (0.79%) to invade sites where supercolonies were suppressed and RLC numbers recovered than at sites where supercolonies remained intact ($P = 0.506$). However, when RLC numbers failed to rebound at baited sites (Baited + low recovery), the probability of GALS invasion was much higher, 72-fold greater than at Intact sites ($P = 0.145$).

The probability of GALS invasion at a focal site was also related to the attributes of neighboring sites (*c* parameters in Table 1; Fig. 2). Sites with high proportions of neighbors that were either Intact or Baited + high recovery (c_1 and c_4), both with abundant

TABLE 1. Parameter estimates for model (Eq. 1) for comparisons of sites invaded by giant African land snails (GALS), 2001–2007, and sites remaining uninvaded over that period.

Parameter, by forest state and by site	Deviation from reference condition (mean ± SD)	Odds ratio†	<i>P</i> ‡
Reference condition			
<i>a</i> , intercept (intact)	−6.02 ± 1.54	inf	0.002
Deviation from reference condition			
Recipient communities			
<i>b</i> ₁ , intact (identified with <i>a</i>)	...		
<i>b</i> ₂ , YCA supercolony	6.05 ± 1.31	inf	0.506
<i>b</i> ₃ , ghosted	2.48 ± 0.89	908.1	0.028
<i>b</i> ₄ , baited + high recovery	0.45 ± 1.44	1.7	0.004
<i>b</i> ₅ , baited + low recovery	4.24 ± 1.26	inf	0.145
Neighboring communities			
<i>c</i> ₁ , neighbors intact	−5.17 ± 1.61	1425.5	
<i>c</i> ₂ , neighbors YCA supercolonies	1.02 ± 2.14	2.1	
<i>c</i> ₃ , neighbors ghosted	1.39 ± 1.62	3.9	
<i>c</i> ₄ , neighbors baited + high recovery	−7.90 ± 2.45	inf	
<i>c</i> ₅ , neighbors baited + low recovery	−0.72 ± 1.88	1.8	
Propagule pressure			
<i>d</i> , total neighbors with GALS previously	8.17 ± 2.12	inf	
<i>e</i> , distance to clearing or roadway	−0.99 ± 0.49	58.5	

† Odds ratios >10 (in boldface type) are important effects; inf stands for infinity.
 ‡ *P* is the probability of invasion by GALS for each of the five states of the recipient community (parameters *a* and *b*_{*i*}), given zero effects of continuous variables (Appendix A). *P* was calculated as exp(parameter mean)/[1 + exp(parameter mean)]. *P* is not calculated for variables *c*–*e* because they are regression coefficients, not effects.

RLC, were very resistant to invasion (Fig. 2). However, the probability of GALS invasion was unrelated to the proportion of neighboring sites that were either YCA supercolonies, Ghosted, or Baited + low recovery.

Propagule pressure also played an important role in determining the probability of GALS invasion. The total proportion of sites in the neighborhood that had been invaded by GALS in the previous time period greatly increased the probability of invasion (*d* parameter in Table 1; Fig. 2). Proximity to clearings (*e*) also was a strong factor leading to elevated probabilities of invasion (Table 1, Fig. 2) but the effect weakened over time as the invasion front of GALS moved into the rain forest (Fig. 1a; Appendix E).

Survival and persistence of GALS

Tethered GALS survived in YCA supercolonies but were rapidly discovered and eaten by RLC in both Ghosted and Intact sites. GALS survived 115 times longer in YCA supercolonies (92.0 ± 57.7 days [mean ± SD] than in Intact sites (0.8 ± 0.6 days) and over 12 times longer than in Ghosted sites (7.4 ± 6.0 days) (Appendix F). Tethered GALS in Ghosted sites survived substantially longer than in Intact sites. Survivorship reflected activity of YCA and densities of RLC. In supercolonies, YCA activity averaged 51.6 ± 2.6 ants per card per 60 seconds (mean ± SE) and RLC were never recorded. YCA did not attack live GALS, although they sometimes fed on dead ones. We

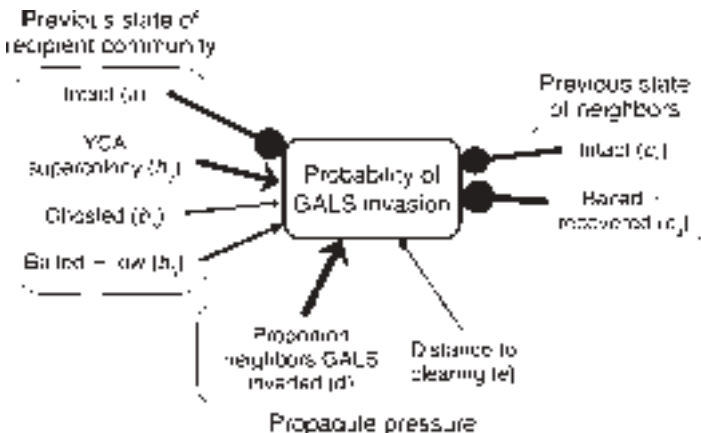


FIG. 2. Important effects determining the probability of invasion by the giant African land snail (GALS), 2001–2007. Effects are categorized by state of the recipient community, neighborhood states, and factors affecting propagule pressure (see Appendix A for model details). Letters in italics (*a*, *b*₂, etc.) refer to model parameters in Table 1; YCA is the yellow crazy ant. Effect size is indicated by the width of lines as determined from parameter estimates (Table 1); positive effects on the probability of GALS invasion are indicated by arrows, and negative effects by solid circles. Unimportant effects are given in Table 1.

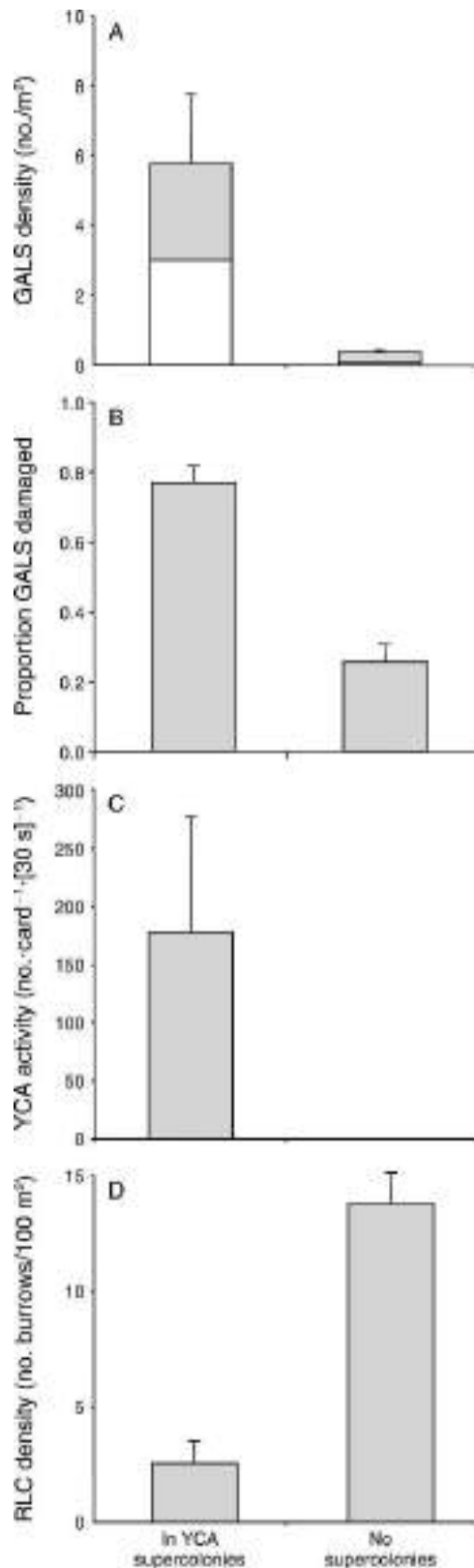


FIG. 3. Persistence of GALS (giant African land snails) in YCA (yellow crazy ant) supercolonies ($n = 6$) or where YCA supercolonies had never formed ($n = 5$). Data are means and

attributed almost all snail mortality to starvation (87%); the bodies of 35% of dead GALS were still in their shells and the remainder of whole shells were empty. Only 2 of 20 GALS at one site were killed by RLC in the initial week; otherwise, no mortality was associated with RLC in YCA supercolonies. In Intact sites, YCA were never recorded and foraging RLC were abundant (averaging 25.4 ± 3.0 crabs/100 m² [mean \pm SE]). Over 87% of snails were eaten by crabs within 24 h; none survived >4 days. In Ghosted sites, YCA were absent and RLC occurred at only a small fraction of the densities seen at Intact sites (0.2 ± 0.1 crabs/100 m²). Nevertheless, these few RLC proved sufficient to kill all snails in Ghosted sites after 20 days.

GALS densities (live and dead snails) were >20 times higher in YCA supercolonies than in sites where supercolonies had not formed (Fig. 3A, Appendix G). Predation pressure by RLC, as indicated by proportion of damaged shells, was >3.5 times greater at sites without YCA supercolonies (Fig. 3B). This reflected absolute differences in activity of YCA between sites with and without supercolonies (Fig. 3C) and the >5-fold difference in RLC burrow densities between sites with YCA supercolonies and those where supercolonies had never formed (Fig. 3D, Appendix G). Adult reproductive snails occurred in all YCA supercolonies and were >13 times as abundant as at sites without supercolonies (Fig. 4). Juveniles were also abundant in most YCA supercolonies, but snails <25 mm in length were not detected at sites without YCA supercolonies (Fig. 4).

DISCUSSION

In this study we integrated several important but poorly understood issues about biological invasions: the role of positive interactions in the ecological success and impact of invaders, their effect in facilitating secondary invasions, and the relative importance of recipient-community attributes and propagule pressure in invasion success. By combining repeated whole-island surveys and management of invader–invader interactions, we showed that mutualistic associations among invaders strongly alter attributes of the native recipient community and increase propagule pressure that pave the way for entry and speed the spread of a secondary invader. Smaller-scale experiments and comparative studies demonstrated that invader–invader mutualism facilitates this secondary invasion by eroding native biotic resistance and creating enemy-free space. We believe this is the strongest empirical evidence yet for the invasional meltdown hypothesis for increased impacts and accelerating rates of biological invasions.

SE. (A) Density of GALS individuals; open portions of bars are live snails and shaded sections are empty shells. (B) Proportion of damaged GALS shells as an index of predation pressure by red land crabs (RLC). (C) YCA activity. (D) RLC density.

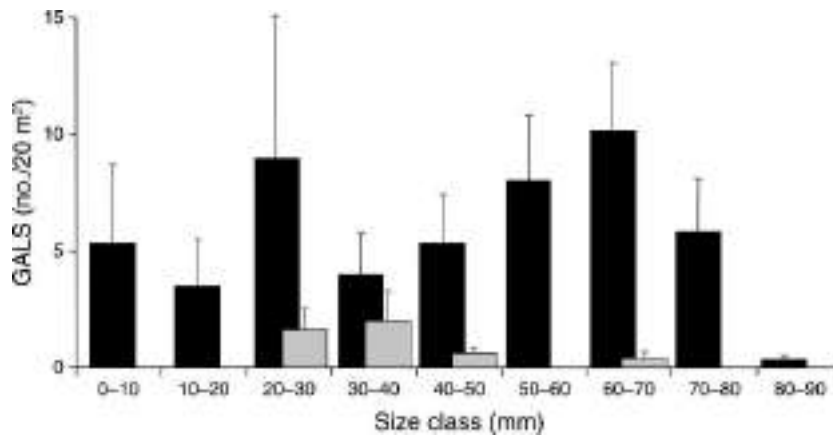


FIG. 4. Composite size-class distributions (mean and SE) of live GALS at waypoints in YCA supercolonies ($n=6$; dark bars) and waypoints without supercolonies ($n=5$; light bars). Live GALS were present at all waypoints at the time of survey. Adult reproductive snails were considered to be >40 mm in length (Raut and Barker 2002).

Positive interactions and invasional meltdown

Positive interactions are increasingly being integrated into evolutionary (Elias et al. 2008, Kikvidze and Callaway 2009) and ecological (e.g., Stachowicz 2001, Bruno et al. 2003, Brooker et al. 2008) theory, including their role in biological invasions (Simberloff and Von Holle 1999, Bruno et al. 2003, Bulleri et al. 2008, Altieri et al. 2010). Invasional meltdown is predicated on positive interactions that amplify invader impacts to facilitate secondary invasions. Although scenarios for invasional meltdown exist (e.g., Best and Arcese 2009, Heimpel et al. 2010, Rodriguez-Echeverria 2010), few studies demonstrate facilitation of populations of co-occurring exotic species, changes in broader interaction networks, or invasion-induced ecosystem impacts (Simberloff 2006, 2011). On Christmas Island, trophic interactions between exotic ant-scale mutualists reconfigured interaction networks (Fig. 5). A positive population-level effect on ants resulting from adventive mutualism generated a “new” predator of the dominant native consumer in island rain forest. The addition of a new trophic level induced a trophic cascade and, by creating enemy-free space, facilitated the entry and rate of spread of a secondary invader. This reconfiguration is likely to facilitate further invasions. The abundance and species density of other alien ant species is higher at yellow crazy ant (YCA)-affected sites than at Intact sites (O’Dowd and Green 2010), and we have observed elevated densities of other alien land snails in YCA supercolonies. Furthermore, several invasive plant species formerly restricted to clearings (e.g., *Muntingia calabura*, *Carica papaya*) have invaded forest with YCA supercolonies. These changes could further alter interaction networks, amplify impacts, and accelerate overall rate of species invasion. Invasional meltdown should no longer be seen as controversial (Gurevitch 2006, Simberloff 2006).

Determinants of invader success

Invasion success can be determined by three key attributes: characteristics of the recipient community, propagule pressure, and species traits (Lockwood et al. 2005, Colautti et al. 2006). While species traits are clearly important, their effectiveness depends on the nature of the recipient community and propagule pressure (Simberloff 2009). Recent analyses show variable results for their relative importance: either abiotic and biotic aspects of the recipient community (e.g., Moyle and Light 1996, DeRivera et al. 2005) or propagule pressure (Von Holle and Simberloff 2005) is paramount; more commonly, interaction between the two is important (e.g., Thomsen et al. 2006, Hollebone and Hay 2007, Sanders et al. 2007, Clark and Johnson 2009, Eschtruth and Battles 2009).

Biotic resistance is an important attribute of recipient communities that affects invasion success (Elton 1958, Catford et al. 2009). Site-specific experiments and surveys in our study demonstrated the strength of biotic resistance provided by RLC against invasion by land snails; in the presence of predatory RLC, GALS was unable to act as a primary invader. We found no evidence for persistent GALS populations (i.e., low overall densities, absence of small size classes, and widespread evidence of predation by RLC) in intact forest, despite high frequencies of occurrence and build-up of impressive propagule densities over 50 years in clearings bordering rain forest (Sproul 1983, Lake and O’Dowd 1991). However, biotic resistance was rapidly eroded wherever YCA supercolonies formed, facilitating GALS entry and spread as secondary invaders. Persistent GALS populations (i.e., high densities, presence of a range of size classes, low predation by RLC) occurred only in YCA supercolonies that confer enemy-free space to GALS, first by strongly suppressing RLC populations and second by preventing RLC recolonization. The presence of a calcified shell, mucous secretion, and the

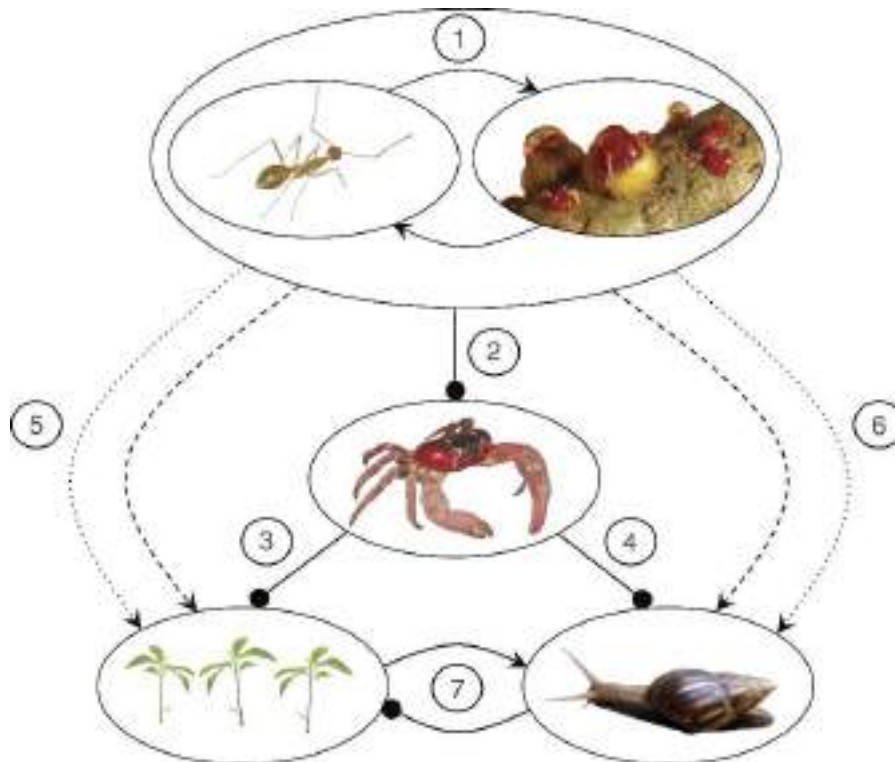


FIG. 5. Interaction pathways by which mutualism between the introduced yellow crazy ant (YCA), *Anoplolepis gracilipes*, and honeydew-secreting scale insects (e.g., *Tachardina aurantiaca*) leads to invasional meltdown and secondary invasion by giant African land snail (GALS) in rain forest on Christmas Island, Indian Ocean. Solid lines are direct effects; dotted or dashed lines are indirect effects. Lines ending in arrows indicate positive effects; those ending in solid circles are negative effects. The circled numbers indicate published evidence or unpublished observations for each interaction: (1) The interaction between YCA and scale insects is mutualistic, leading to population explosions of both (O'Dowd et al. 2003, Abbott and Green 2007), which (2) suppress local populations of the native red land crab *Gecarcoidea natalis* (O'Dowd et al. 2003). (3) Red crabs are key regulators of seedling abundance and diversity (Green et al. 1997, 2008) and (4) prevent the exotic giant African land snail, *Achatina (Lissachatina) fulica*, from establishing in intact forest by eating them (Lake and O'Dowd 1991; our present study). By suppressing red crabs, YCA and scale insects (5) promote indirectly the mass recruitment of seedlings and accumulation of litter (O'Dowd et al. 2003) as key resources for GALS, while (6) simultaneously creating enemy-free space for GALS. Although GALS is a generalist herbivore, its impacts on (7) native seedling abundance and diversity remain unquantified. The indirect effects of ant-scale insect mutualism on seedling recruitment and invasion by GALS occur both in YCA supercolonies (dashed lines) and at Ghosted sites remote from supercolonies (dotted lines).

ability to seal the operculum did not provide effective defense against RLC, but these very traits were likely to protect GALS from YCA.

These experiments and surveys provide a mechanistic understanding for invasion dynamics played out at a whole-island scale. The strong negative effect on invasion probability of Intact sites is consistent with high densities of RLC (a) while positive effects in YCA supercolonies (b_2) and Ghosted (b_3) sites is consistent with their absence (the smaller effect size in Ghosted sites is related to their slightly higher densities of RLC). Furthermore, whole-island suppression of YCA supercolonies (Green and O'Dowd 2009) provided experimental confirmation for the importance of the recipient community; suppression of YCA following aerial baiting reversed the probability of GALS invasion, reinstating biotic resistance by permitting RLC to recolonize some areas of forest.

Changes in resource levels in recipient communities can also influence invasion success (Davis et al. 2000, Davies et al. 2007, Rowles and Silverman 2009). Although YCA clearly facilitate invasion by GALS by eliminating their key predator, they may also facilitate invasion by increasing resource availability. Seedlings and leaf litter provide both food and habitat for land snails, both of which are consumed by RLC as an herbivore-detritivore. Suppression of RLC in YCA supercolonies results in a 30-fold increase in seedling abundance and doubles leaf litter cover (O'Dowd et al. 2003). Furthermore, removal of RLC buffers variation in litter availability (Green et al. 1999), which would stabilize seasonal fluctuations in both habitat and food availability for GALS.

While propagule pressure has frequently been shown to be a key determinant for successful establishment of invaders (Lockwood et al. 2005, Colautti et al. 2006,

Simberloff 2009), our study shows that it can be important in propagating the spread of invaders. In the early stage of GALS invasion of rain forest, the proximity of sites to clearings and roads, the original source areas of GALS, was important. However, as the invasion front moved further into the forest, the probability of GALS invasion at a site increasingly depended on the frequency of occurrence of GALS in neighboring sites. Logically, the state of sites in a neighborhood should determine their capacity to limit the spread of GALS or to act as “donor” sources. A high proportion of neighbors that were either Intact or Baited + high recovery surrounding a focal site had an important inhibitory effect on GALS invasion probability, consistent with the notion that high densities of RLC in surrounding areas provides a strong layer of biotic resistance, regardless of the state of the focal site. Conversely, low biotic resistance at this neighborhood scale (YCA supercolonies) did not facilitate GALS invasion at a focal site. This is puzzling because persistent, high densities of GALS build up in some YCA supercolonies that should act as donors to focal sites. This could be explained by the fact that most YCA supercolonies had not been invaded at early stages of GALS spread and that subsequent management intervention drastically reduced the number of YCA supercolonies that could otherwise act as sources for GALS. This could have limited our ability to detect a neighborhood effect of site state on the probability of GALS invasion. Although we could not explicitly test for relative importance of recipient-community attributes against propagule pressure (e.g., Tanentzap and Bazely 2009), we argue that islandwide changes in the recipient community have triggered this secondary invasion by creating enemy-free space for GALS, and that interaction between the state of the recipient community and propagule pressure was the key in propagating the invasion.

*Management of positive interactions
and ecosystem restoration*

Identification of interaction networks among invasive species offers opportunities beyond a single-species approach for mitigation of impacts and ecosystem restoration in multiply invaded systems (Bull and Courchamp 2009). Dissolution of mutualism between invaders should disrupt positive population-level feedback and mitigate impacts. If affected populations of native species have sufficient resiliency and dispersal powers, restoration of “pre-meltdown” populations and interaction networks should be feasible. On Christmas Island, ongoing, whole-island suppression of this exotic ant–scale mutualism, either by use of toxic ant baits (Green and O’Dowd 2009; Boland et al., *in press*) or through introduction of biological control agents to suppress scale-insect densities (Lester 2008) should eventually lead to the widespread recovery of RLC populations, reversion of recipient communities to pre-

invasion status, and the reversal of GALS invasion. Management of “facilitator species” (Heimpel et al. 2010), like the YCA and scale insects, has important implications for reversal of the impacts of invasional meltdown by restoring the recipient community.

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APPENDIX A

Bayesian modeling of forest states and probability of invasion by giant African land snails (GALS) (*Ecological Archives* E092-150-A1).

APPENDIX B

Description and rationale for assignment of waypoints to forest states in the island-wide survey (*Ecological Archives* E092-150-A2).

APPENDIX C

Bayesian modeling of survival of tethered GALS (*Ecological Archives* E092-150-A3).

APPENDIX D

GALS density and predation pressure in and out of any supercolonies (*Ecological Archives* E092-150-A4).

APPENDIX E

A table presenting parameter estimates for model A.1 (in Appendix A) for comparisons of sites first invaded by GALS in the periods 2001–2003, 2003–2005, and 2005–2007 (*Ecological Archives* E092-150-A5).

APPENDIX F

A table presenting parameter estimates for model C.1 (in Appendix C) for comparisons of survival time (indays) of tethered GALS in three forest states (yellow crazy ant [YCA] super colonies, intact forest, and ghosted forest) over 180 days (*Ecological Archives* E092-150-A6).

APPENDIX G

A table presenting parameter estimates for model D.1 (in Appendix D) for comparisons of GALS density (live individuals and total shells), the proportion of broken GALS shells, YCA activity, and red land crab (RLC) burrow density (*Ecological Archives* E092-150-A7).