Box 15.1 Invasional meltdown: do invasive ants facilitate secondary invasions? Dennis J. O'Dowd and Peter T. Green AQ4

Biological invasions can fundamentally alter the structure, composition, dynamics, and function of natural ecosystems. Direct and indirect effects of some invaders can be so pervasive and strong that these reconfigure entire interaction networks and lead to state changes in ecosystems (Croll *et al*. 2005). Simberloff and von Holle (1999) go still further to suggest that they can lead to 'invasional meltdown' whereby invader–invader synergism amplifies and diversifies impacts so as to facilitate secondary invasions and further accelerate impacts. The invasional meltdown metaphor remains controversial: Few studies have demonstrated conclusively that synergies between invaders pave the way for secondary invasions.

Invasive alien ants frequently have large and varied impacts on natural ecosystems. This may be especially so on islands where native species richness and functional redundancy are low, and propagule pressure can be high. Some invasive ants form expansive supercolonies with high, sustained densities of worker ants that extend from hectares to many square kilometres. The invasion and supercolony formation by the yellow crazy ant, *Anoplolepis gracilipes* (YCA hereafter) in rainforest on Christmas Island (Indian Ocean) is a notable example of the manifold impacts of a single invader on a natural ecosystem. On the forest floor, this ant attacks and kills the dominant native omnivore, the red land crab, *Gecarcoidea natalis* (O'Dowd *et al*. 2003). In the forest canopy, YCA forms new mutualistic associations with herbivorous, honeydew-secreting Hemiptera (Abbott and Green 2007). These effects change the network and strength of interactions among producers, herbivores, and detritivores, deregulating seedling recruitment, increasing tree mortality, reducing litter decomposition, and affecting higher-order consumers such as birds (Davis *et al*. 2008; O'Dowd *et al*. 2003).

Does this qualify as an invasional meltdown as defined by Simberloff (2006)? True meltdowns comprise two distinct but complementary components. First, invader–invader interactions should generate positive population-level feedbacks that amplify impacts. There seems little doubt that interactions between YCA and honeydew-secreting scale insects sustain elevated populations of both that go on to amplify impacts. Second, impacts resulting from this synergism should enhance secondary invasions. We evaluate this second criterion by considering whether YCA invasion promotes invasion by an alien snail and facilitates the broader assemblage of introduced ants on the island.

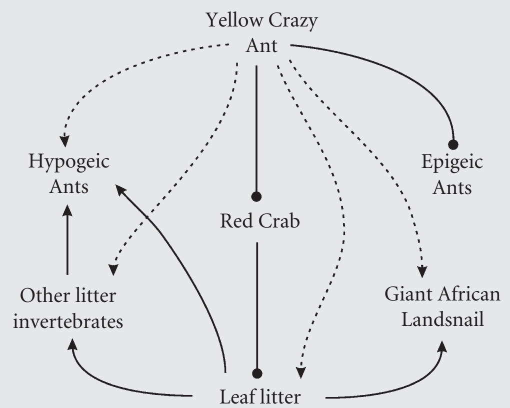

Figure 15.1.1 Interaction pathways by which invasion and supercolony formation by the yellow crazy ant, *Anoplolepis gracilipes* (YCA) facilitate other invaders on Christmas Island. Solid lines are direct effects, dashed lines are indirect effects; arrows are positive effects; knobs are negative effects. The YCA invasion facilitates secondary invasion of rainforest by the giant African landsnail (GALS) and hypogaeic ants through its impacts on omnivorous red land crabs. Red crabs are both predators of GALS and regulators of litter breakdown. By extirpating red crabs, YCA releases GALS from predation pressure, allowing entry into primary forest and the build-up of a key resource, litter. The abundance and diversity of hypogaeic ants are also facilitated by litter build-up that provides habitat, food resources, and a refugium from the epigaeic YCA. However, the YCA also has direct and adverse effects on some epigeic ants, probably through interference and exploitative competition. AQ5

The giant African land snail (*Achatina fulica*, GALS hereafter), a noteworthy invader throughout the tropics, has been present on Christmas Island for decades. However, it never managed to penetrate intact primary rainforest, despite its widespread distribution in disturbed habitats across the island. The reason is

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Box 13.1 continued

simple: predaceous native red crabs are a formidable barrier to snail invasion of primary rainforest (Figure 15.1.1). Experiments show that red crabs rapidly discover tethered GALS and devour them within hours (Lake and O'Dowd 1991). The YCA, by extirpating red crabs, allow GALS to breach the barrier and establish in primary forest. Tethered snails persist in YCA supercolonies for months, with 53 ± 6 % (SE, *N* = 3 sites) survival after 60 days. Some even produce egg masses. In contrast, all snails tethered in uninvaded sites were killed and eaten by red crabs after just 6 days. In the wake of widespread invasion by YCA, we now see GALS invading primary rainforest in many locations across the island.

The ants of Christmas Island – a synthetic assemblage – comprise the flotsam and jetsam of the ant world. Elsewhere, invasive ants are typically seen to disrupt and deplete ant diversity. However, the reverse is true on Christmas Island: YCA invasion indirectly facilitates increased abundance and species density of non-native ants in island rainforest. On a per-area basis, ant abundance is three-fold greater in invaded sites (33.6 ± 9.2 ants m^{-2}) than in uninvaded sites (9.5 ± 2.0 ants m^{-2}; $F_{2,12}$ = 12.88, P = 0.001). Likewise species density was twofold greater in invaded sites (2.4 ± 0.2 species m^{-2}) than in uninvaded sites (1.0 ± 0.1 ants m^{-2}; $F_{2,12}$ = 7.98, P = 0.006). However, differences in species density but not abundance disappear when differences in litter mass between site types are considered. When expressed on a per kilogram litter basis, the abundance of other ants was still twofold higher in invaded sites ($F_{2,12}$ = 11.65, P = 0.002), but there was no difference in species richness ($F_{2,12}$ = 0.14, P = 0.872). Strong compositional differences also occurred between ants in YCA-invaded and uninvaded sites (Global R = 0.521, ANOSIM P = 0.008).

These impacts of the YCA on the diversity of other ants are largely indirect and mediated by its effects on litter (Figure 15.1.1). By eliminating the red crab, which otherwise regulates leaf litter on the forest floor, YCA invasion increases litter biomass and, thus, habitat and food for other ants, especially small litter-foraging (i.e. hypogaeic) species. Nevertheless, the YCA does disrupt a few surface-foraging (i.e. epigaeic) ants so can also directly affect species composition. These results illustrate invasional meltdown whereby direct interaction between the YCA and the red crab, itself accelerated by YCA-scale mutualism, facilitates the rapid population increase and local species richness of other introduced ant species.

We argue that these data demonstrate invasional meltdown *sensu stricto* (Simberloff 2006). For us, invasional meltdown is a real phenomenon and a most fortunate metaphor (cf. Gurevitch [2006]), evocative of complex changes that can be wrought by biological invaders in general, and invasive ants in particular.

vulnerable because they can suffer from direct predation as well as competition for prey (P. Krushelnycky and R. Gillespie, unpublished data). However, elsewhere, evidence for effects of invasive ants on spiders and other carnivores is mixed (Holway *et al*. 2002a; Table 15.1). Several early studies showed increases in scavenger abundance in invaded areas, but the study designs precluded ruling out disturbance to the sites as the primary cause (Human and Gordon 1997 and references therein). Species-level analyses will be necessary to elucidate the species that are truly vulnerable and the traits or contexts that inure native species to displacement by invasives.

Some ground-dwelling invertebrates that prey on ants have benefited from ant invasions. Myrmecophagic spiders in Japan (Touyama *et al*. 2008) and ant-lions in California (Glenn and Holway 2008) have responded positively to Argentine ant invasions (Table 15.1). The higher abundance of invasive ants relative to the displaced native ants appears to be a key feature driving the benefits to these organisms.