Citation: Gruber MAM, Burne AR and Cooling M. 2025. Biology and Impacts of Pacific Islands Invasive Species. 19. *Anoplolepis gracilipes*, the Yellow Crazy Ant (Hymenoptera: Formicidae) Pacific Science. 2025. 79(3) xx-xx

Biology and Impacts of Pacific Islands Invasive Species. 19. *Anoplolepis gracilipes*, the Yellow Crazy Ant (Hymenoptera: Formicidae)[1]

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Abstract: *Anoplolepis gracilipes* (yellow crazy ant), among the world's most damaging invasive ants, and likely native to southeast Asia, occurs in ~90% of countries and territories in the tropical Pacific islands region. Several characteristics contribute to their socioeconomic and environmental impacts, which primarily affect people's wellbeing, agriculture, and biodiversity. Unpredictable, sometimes repeated, population outbreaks are often observed. They use formic acid for defense, and when in large numbers this enables them to overwhelm prey and competitors. Competition is the major population regulator among ants, and high abundance enables yellow crazy ant populations to dominate other ants. Their abundance is compounded by monopolization of carbohydrate resources, often through mutualisms with honeydew producing insects. Tolerant of diverse habitats, the ants are likely to increase in distribution with climate change. The best management option, preventing arrival, is possible in only a few locations in the region. Where they are already present, the arrival of new populations should be avoided. Biosecurity efforts should also focus on reducing domestic spread among islands and preventing the arrival of new mutualists. Eradication of yellow crazy ants requires toxicants with potential non-target impacts, and often fails, or is prohibitively expensive. Long-term monitoring and effective biosecurity are essential to ensure the ant's

[1] Manuscript accepted 17 April 2025

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continued absence after eradication. The recent interest in genomic approaches to invasive ant control shows promise, as does the use of viruses and other micro-organisms. However, these tools are far from operational. We outline recommendations to improve the management of yellow crazy ant in the region.

INTRODUCTION

Interest in the impact and management of invasive ants has increased markedly since James Wetterer said in his Pacific Science review of African big-headed ants (*Pheidole megacephala*), "Perhaps due to their small size, they are usually not taken very seriously. This is a mistake" (Wetterer 2007). In the intervening period, we have seen the development of several strategies and plans to prevent the movement of invasive ants into and around the Pacific (e.g., Vanderwoude et al. 2021, Hoffmann et al. 2024). As well as improvements in methods of control and possible eradication (e.g., Hoffmann et al. 2011, Buczkowski et al. 2014, Peck et al. 2017, Tay et al. 2017), we have a better understanding of their impacts in the region (e.g., Loope and Krushelnycky 2007, Wetterer 2007), and globally (e.g., Angulo et al. 2022, Gruber et al. 2022, Montgomery et al. 2022). Despite this increase in awareness and knowledge, invasive ants continue to cause problems and spread in the Pacific islands region.

Of the five most concerning invasive ants globally (Gruber et al. 2022), in the last 20 years, little fire ants (*Wasmannia auropunctata*) have expanded the most to new countries and territories in the Pacific islands region (Gruber et al. 2017, Montgomery et al. 2022). Red imported fire ants (*Solenopsis invicta*) have not yet reached the tropical Pacific islands region and Argentine ants (*Linepithema humile*) are found primarily in Pacific rim countries, and many of their offshore islands, as well as Hawai'i, Norfolk Island, and Rapa Nui (Felden 2025). The remaining two species of the five most concerning ants globally, African big-headed ant and yellow crazy ant (*Anoplolepis gracilipes*), have been in the Pacific islands region since some of the earliest published surveys (Wilson and Taylor 1967, Wetterer 2005, 2007).

The yellow crazy ant is so ubiquitous that it was occasionally considered to be native to western Pacific islands, although the consensus for the native range is southeast Asia (Wetterer 2005, Chen 2008). Known for repeated and often unpredictable population outbreaks (Lester and Gruber 2016 and references therein), the ant can reach extremely high numbers in the region (Lester and Tavite 2004, Hoffmann et al. 2014, Burne and Gruber 2017, Gruber et al. 2018) and elsewhere (e.g., O'Dowd et al. 2003). Ant nest density is arguably the best measure of population density. However, counting nests is often not practical, due to the effort involved, particularly in developing countries

and territories. Therefore, outbreaks are typically quantified using *card counts*, a neutral measure of ground foraging worker activity (Green et al. 2004). However, often these outbreaks are typically first assessed qualitatively by the people who experience them, when the ant reaches high enough abundance so that daily life is disrupted or impacts on plants and animals are perceived.

When in high abundance the ants can dominate the natural environment, and cause harm to all sectors of human interest, including conservation of biodiversity, infrastructure, agriculture, and well-being (Gruber et al. 2022). Many people who have not experienced these outbreaks do not recognize yellow crazy ants as a potential problem. As James Wetterer said in 2007, this is a mistake.

In this review we outline key aspects of the yellow crazy ant's biology and ecology that contribute to its ecological, economic, and well-being impacts. We add detail to previous reviews of the species, including its distribution in the Pacific islands region (Wetterer 2005, Gruber et al. 2017), ecology, and management (Lee and Yang 2022), and make recommendations to reduce its threat and potential impact in the region.

NAME

Anoplolepis gracilipes (Smith, F., 1857), is known by several common names in the Indo-Pacific region (O'Dowd 2009), including yellow crazy ant (the most widely used English name), ashinaga-ki-ari (Japanese), gramang ant (Indonesian), long-legged or longlegged ant (English, derived from its former scientific name *A. longipes*), Maldive ant (English-Seychelles), Gelbe Spinnerameise (GISD 2024, German translation of yellow crazy ant), and la fourmi folle jaune (French translation of yellow crazy ant). Crazy ant was used in the past, but is less common and not recommended due to the confusion with the brown/black/long-horned crazy ant (*Paratrechina longicornis*), which was also known as crazy ant (Wetterer 2005).

Although yellow crazy ant is the most often used name in the Pacific islands region, the terms long-legged or, less commonly longlegged, ant are also used, and the latter is preferred by the Entomological Society of America (Lee and Yang 2022). The name longlegged ant appears in the abstract of eight citations in FORMIS 2024a (Wojcik and Porter 2024), long-legged ant appears in 15, and yellow crazy ant appears in 90. As longlegged ant is not typically used outside the United States (and not regularly used in Hawai'i) it could cause confusion, so we use the name yellow crazy ant in this review.

The synonym *Anoplolepis longipes* (Jerdon) was often used until recently (see references in FORMIS 2024a, Wojcik and Porter 2024), and will likely be found occasionally in the future, particularly in non-science publications. Earlier names also included *Formica longipes* Jerdon, 1851 and *Formica gracilipes* Smith, F. 1857a. Bolton et al. (2007) provide a full history of the naming of the genus and species.

DESCRIPTION AND ACCOUNT OF VARIATION

Anoplolepis gracilipes (sub-family Formicinae) is one of only nine species (some with subspecies) in the genus (Bolton et al. 2007). The other eight species are *A. carinata, A. custodiens* (nominal species and three subspecies) *A. fallax, A nuptialis, A. opaciventris, A. rufescens, A. steingroeveri* (nominal species and two subspecies), and *A. tenella* (Bolton et al. 2007). Although the other species of *Anoplolepis* all have African/Arabian/Western Indian Ocean distributions, yellow crazy ant is not found anywhere in those regions except South Africa, where it is considered to be introduced (Ndaba et al. 2023). As yellow crazy ant is the only species of *Anoplolepis* in the Pacific islands region, it is unlikely to be confused in the field with other ants of the same genus.

As with most ant species, yellow crazy ants have three known life-forms (sometimes called castes): queens, workers, and males. Queens and males are rarely seen, unless a nest is disturbed, or when winged queens are seen flying. As the ant is relatively large and distinctive in movement, identification is easily confirmed with workers (Figure 1).

<> Figure 1<>

Species Description

Yellow crazy ant workers are monomorphic (all closely similar in size) and approximately 4-5 mm long (excluding legs and antennae, Figure 1). They have slender bodies (head, thorax, and gaster, or abdomen) with long legs and long 11-segmented antennae. Antennal scapes are > 1.5 times longer than the width of their relatively small head. The eyes are relatively large and wideset, breaking the outline of the head when viewed face-on. Queens are approximately 10 mm long and have a robust appearance (Figure 1, Figure 2), while males are approximately the same size as workers, but have wings (Figure 2). The queen's wings are lost once she has mated and founded a new nest.

The ant's color varies from a muted yellow to a golden brown, and typically the gaster is darker than the head and body. The ant does not have any spines on its thorax and the body appears smooth, with few visible hairs. It has a single-segmented petiole (waist) between the thorax and gaster. Like all other Formicine ants, the yellow crazy ant does not have a stinger, rather it has an opening at the

tip of the gaster, the acidopore, through which it releases formic acid. Release of formic acid is used to overcome prey and for defense from other ants, including unrelated populations of conspecifics. More detailed technical descriptions of yellow crazy ant anatomy can be found in Wetterer (2005), and using the PIAkey (Sarnat 2008).

<> Figure 2<>

Distinguishing Features

The yellow crazy ant is fairly easy to recognize in the field in the Pacific islands region. The ants are very fast-moving, and their erratic movements when disturbed are emphasized by their relatively long antennae and legs. The ant gets its most frequently used common name from the way it scatters when disturbed, together with its golden yellow coloring.

In the Pacific islands region there are few other species that yellow crazy ant can be confused with (Sarnat 2008). The longhorn (black) crazy ant *Paratrechina longicornis* also has relatively long antennae and erratic movements, but it is slightly smaller and much darker than the yellow crazy ant and is also covered with sparse dark hairs. *Camponotus* spp. (usually in the *C. maculatus* group in the region) are similarly colored, but are larger, with a more robust appearance than the yellow crazy ant. Also, species in the *C. maculatus* group are polymorphic, i.e., with two distinctly different worker life forms (castes), with the major workers having disproportionately larger heads than the minor or media workers. It is usually straightforward to confirm the identification with the naked eye or a hand lens. Sarnat (2008) developed an excellent guide to compare the three species.

RESOURCE REQUIREMENTS AND LIMITATIONS

The yellow crazy ant's chief resource requirements are nesting and food. They are indiscriminate generalists for both resources. The ants have been found nesting in or under many materials, including leaf litter, rocks, fallen vegetation cracks and crevices (Room 1975, Lewis et al. 1976, Haines and Haines 1978a, Rao and Veeresh 1991). In addition, on atolls such as Tokelau and Tuvalu they use rotting coconuts (authors observations), urban structures, such as warehouses, trash, and the base of trees (Lester and Tavite 2004). In Papua New Guinea, Tokelau and Zanzibar, they nest underground (Baker 1976, Lester and Tavite 2004), but this is likely because the soil substrate is suitable (Haines and Haines 1978a). They also nest in trees in cacao agroforestry sites (Bos et al. 2008) and in coconut canopies (Young 1996, Lester and Tavite 2004). The ant does not nest inside houses in the region (Lester and Tavite 2004, Gruber et al. 2013).

Diet

As with many invasive ant species, the yellow crazy ant has a broad dietary range, is an effective hunter in larger numbers, an opportunistic scavenger, and highly efficient at monopolizing carbohydrate resources. Ants typically require more protein resources when queens and males are being produced. In the Seychelles, no seasonal changes were observed (Haines and Haines 1978a), but Abbott et al. (2014) found that food preferences on Christmas Island aligned with seasons, with some variation. At the beginning of the dry season the ants either foraged without preference for carbohydrates or protein, or more commonly showed a moderate preference for protein. They preferred carbohydrates throughout the wet season. Foraging patterns have not been studied in detail in the Pacific islands region.

Carbohydrate Sources

Carbohydrates are essential for all ants, and these resources, often obtained through extra-floral nectaries or by tending honeydew producing scale insects and other plant pests, contribute to the success of invasive ants, including yellow crazy ants (e.g., Wittman et al. 2018). Yellow crazy ants obtain sugars from plant exudates, honeydew-producing insects and fruit (e.g., Haines and Haines 1978a). Yellow crazy ants can consume and transport vast amounts of these resources. For example, in the Seychelles, up to 50% of the weight of workers was from honeydew they had ingested (Haines et al. 1994).

Yellow crazy ants are well known for novel interactions with plant pests in their invaded range. Their most extreme and widely-known impact, that of ecological meltdown on Christmas Island, was driven by relationships with scale insects (O'Dowd et al. 2003). Four species of honeydew-producing scale insects were abundant and essential carbohydrate sources for yellow crazy ants on Christmas Island (Neumann et al. 2016), and another 11 species of scale and mealybug were tended by the ants (Table 1). Many of these species or their congeners are already in the Pacific islands region, and prevention of their spread should be a priority. Any of these species could be contributing to undetected or unreported impacts, particularly *Coccus hesperidum* and *Saissetia coffeae*, which are present. *Cerococcus indicus, Coccus celatus, Dysmicoccus finitimus* and *Tachardina aurantiaca* are not yet in the region, and prevention of their arrival should be a high priority for biosecurity.

<Table 1>

Interactions between yellow crazy ants and novel carbohydrate resources have been observed often in the Pacific islands region (e.g., Lester and Tavite 2004, Savage et al. 2009, Savage and Rudgers 2013, Burne and Gruber 2017). However, the ants do not consistently use these resources when they are present, the associations vary over time, or there is no association between ant abundance and the resources.

Yellow crazy ants in cocoa plantations in Papua New Guinea were thought to be so dependent on scale insects that ant populations could not be sustained without them (Baker 1972). But in Nu'utele, Samoa, Hoffmann et al. (2014) found several scale and mealybug species in a yellow crazy ant infested area, but interactions were only observed with unidentified scales on Indian mulberry/nonu/noni (*Morinda citrifolia*), and with unidentified mealybugs on coconut. Although the authors found six plant species with accessible carbohydrate sources, yellow crazy ants were only found on nonu and beach hibiscus (*Hibiscus tiliaceus*). In Tuvalu, Halling (2023) found the ants tending nigra scale (*Parasaissetia nigra*) or a similar species, although this was only on specific trees and not widespread. In Hawai'i, Wetterer (1997) found that the ants tended sap-sucking insects on introduced *Cecropia* trees, but they did not use the plants' food bodies – small nutrient-rich structures containing oil droplets and reducing sugars, that some tropical plants have – and which attract ants.

Relationships between yellow crazy ants and honeydew producing insects can change over time. For example, Lester and Tavite (2004) found that where yellow crazy ants were abundant in Nukunonu, Tokelau, they consistently formed relationships with aphids, scale insects, or mealybugs. But 10 years later, this relationship was no longer observed (Gruber et al. 2013). On Motu Aie in Tetiaroa atoll, French Polynesia, the ants tended scale insects (possibly a *Pulvinaria* species, P. Green, personal communication) in 2016, but the ants were not in high abundance (Gruber and H. Jourdan, unpublished data). In February 2019 the scales were being tended by yellow crazy ants (J-Y. Meyer, personal communication), and *Cryptolaemus montrouzieri*, known as the mealybug killer, was also present (G. Jackson, personal communication, Figure 3). By April 2019, the ants were not tending scale insects (G. Bellis, personal communication), indicating that the importance of these relationships vary over time, possibly due to seasonal variation in dietary needs.

Yellow crazy ants are not entirely dependent on these relationships outside the Pacific islands region (Way 1953, Greenslade 1971a), and they can reach very high abundances in the Pacific islands region without them (Gruber et al. 2013, Hoffmann et al. 2014, Gruber et al. 2018). Understanding

the different ecological processes that underpin these relationships and population dynamics would help management of the ant.

<>Figure 3<>

One relationship that is consistently reported is the use of nonu/noni extrafloral nectaries (*Morinda citrifolia*, Figure 3), with or without plant pests present (Lester and Tavite 2004, Savage et al. 2009, Hoffmann et al. 2014). Throughout the region, even when yellow crazy ants are sparse and difficult to detect, they are routinely found on this plant (authors' observations; R. Pierce, personal communication). *Morinda citrifolia* is native to Southeast Asia, and was spread across the Pacific by Polynesian sailors (Pieroni 2005), which could have been a pathway for the ant's expansion in the region, and could help explain their long presence and ubiquity.

Protein Sources

As well as the amino acids and sugars obtained through plant exudates (Haines and Haines 1978a), yellow crazy ants are efficient scavengers, and, at high abundance, also effective predators (Figure 4).

Invertebrates killed and/or consumed by yellow crazy ants include cockroaches, centipedes, corpses of other ants and their own species (Haines and Haines 1978a). At high numbers they are easily able to overcome other ants (Haines and Haines 1978a), and overwhelm and kill Christmas Island red land crabs (*Gecarcoidea natalis*) that are over 100 times an ant's biomass (Abbott 2005), and even larger coconut crabs (Gruber et al. 2018).

In the Pacific islands region, the ants kill and eat a range of vertebrates including seabird chicks, poultry chicks, and lizards (Gruber et al. 2018, Plentovich et al. 2018). Their indiscriminate diet and ability to overwhelm many animals when at high abundance drives many of their impacts in the region (Figure 4, Figure 5).

<> Figure 4<>

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACTS

Yellow crazy ants have significant negative environmental and socioeconomic impacts (Gruber et al. 2022). However, a few isolated positive effects have also been reported, primarily their effectiveness as biological control agents. The impacts of yellow crazy ants on resident ants, other invertebrates and vertebrates are most often density dependent (Hill et al. 2003, McNatty et al. 2009,

Davis et al. 2010, Hoffmann and Saul 2010, Boland et al. 2011, Gruber et al. 2013, Gruber et al. 2018, Plentovich et al. 2018).

The standardized rapid assessment of yellow crazy ant abundance uses a neutral measure of activity whereby the number of ants crossing a 10 x 10 cm white card during a 30 second period provides an estimate of their relative abundance (card counts, Green et al. 2004). Even when the ants are obviously present, card counts can be zero, and the average of a series of counts along a transect usually provides a better indication of abundance. In Tuvalu, an average card count of 45, with point counts between zero and 93, was found on an islet carpeted with the ants (Gruber and Panapa, unpublished data). To detect impacts at lower abundance, other techniques have been used, including baited cards (McNatty et al. 2009, Kaiser-Bunbury et al. 2014, Lach et al. 2022). However, these methods are often study-specific and cannot be used to compare abundances among studies.

The highest card counts (up to 136 in published accounts; equivalent to more than 2,000 ants/m^2) have been recorded on Christmas Island (Abbott 2005), where counts greater than 37 have been used as a threshold for management of the ant, i.e., the point above which they are having impacts on native land crabs (Boland et al. 2011). Card count impact thresholds can vary among taxa. For example, in Atafu, Tokelau, white tern nesting success was sensitive to lower yellow crazy ant abundance, including card counts of zero (Gruber et al. 2018). On Nu'utele islet, Samoa, card counts ranged from 30 to 83 and impacts on ants and other insects were positively density-dependent (Hoffmann et al. 2014). The method can also be used to estimate the success of treatment efforts, with reductions in card count numbers of up to ~95% observed within 3 days of baiting (authors and colleagues, unpublished data). A detailed description of the card count method is available on the Pacific Invasive Ant Toolkit (Gruber et al. 2025).

In a global survey of the impacts of invasive ants, yellow crazy ants were one of the three worst for both environmental and socioeconomic impacts, with an overall ranking as second-worst behind red imported fire ants (Gruber et al. 2022). The scale of impacts seen on Christmas Island, where ant-scale mutualisms have driven a complete ecological transformation (O'Dowd et al. 2003), have not been seen in the Pacific islands region. However, impacts have been reported from Fiji, New Caledonia, Papua New Guinea, Samoa, the Solomon Islands, Tokelau and Hawai'i (references herein). The ant has caused substantial biodiversity impacts in French Polynesia (T. Ghestemme, personal communication), yet these either remain unrecorded in peer-reviewed journals or are recorded in French, which are likely to be overlooked by English-speaking researchers.

Underestimation of impacts is also likely for the other French affiliated territories, Wallis and Futuna, and New Caledonia, as well as remote islands and developing territories and countries.

Impact on Plants

In the Pacific islands region, there have been fewer reports of the effects of yellow crazy ant on native plants than on animals. In Hawai'i the ants robbed more nectar from the native 'Ōhi'a, *Metrosideros polymorpha*, than other invasive ants, potentially excluding the native nectivorous birds that pollinate the plant (Lach 2005). In Samoa, nonu growth was 3,000% higher at sites dominated by yellow crazy ants, and was amplified further when honeydew producing insects were present. The growth of nonu may have been influenced by yellow crazy ants defending the plants against herbivores, although this effect was not significant (Savage and Rudgers 2013). The impact of other users of extra-floral nectaries, or predators of honeydew producing insects was not investigated. Nonu is native to the region, but increased growth of the plant could change ecosystem dynamics, particularly if other plants are negatively affected by yellow crazy ants. For example, in Atafu, Tokelau, yellow crazy ants were thought to kill valued Paina, or ironwood trees (*Casuarina equisitifolia*) by burrowing under the trees and undermining their root systems (Gruber et al. 2018).

It would be prudent to be concerned about newly arriving plant pests that could have mutualisms with yellow crazy ants. Although the importance of the yellow crazy ant/plant pest mutualism is not ubiquitous in the region (e.g., Lester and Tavite 2004, Savage et al. 2009, Gruber et al. 2013, Savage and Rudgers 2013, Burne and Gruber 2017), we know from elsewhere that the arrival of these pests can result in dramatic ecological changes. For example, yellow crazy ants were considered to be relatively harmless on Christmas Island until the arrival of the yellow lac scale (*Tachardina aurantiaca*), which drove ecological transformation on the island (O'Dowd et al. 2003), and other scale insects were involved to a lesser degree. A complete list of potential yellow crazy ant mutualists (or their full range of hosts) has not been determined; however some relationships have been documented, which help to identify risks for the Pacific islands region (Table 1).

The green shield scale insect *Pulvinaria urbicola*, is of concern for the region, as together with yellow crazy ants it was reported to cause the death of birdcatcher trees (*Pisonia grandis*) in the Seychelles (Hill et al. 2003). *Pisonia grandis* is one of the region’s most important native trees. *Pulvinaria urbicola* is already decimating *P. grandis* on Rose Atoll, American Samoa, where yellow crazy ants are not present (Peck et al. 2014).Yellow crazy ants are found elsewhere in American

Samoa, and preventing their arrival on Rose Atoll is a priority, as they could worsen the threat to *Pisonia*.

Impact on Animals

Interactions of yellow crazy ants with other ant species are frequently studied, and their impacts can range from undetectable (Gruber et al. 2013, Hoffmann et al. 2014) to significant (Lester and Tavite 2004, Ward and Beggs 2007, Berman et al. 2013). Common ants might be more severely impacted (Gruber et al. 2018). Smaller ants avoid impacts through differential resource use (e.g., Sarty et al. 2006), while large predatory ants like the trap-jaw ant *Odontomachus simillimus* could be worst affected (Hoffmann et al. 2014). Although the impacts reported have been primarily on introduced ant communities, native ant diversity was reduced in New Caledonia (Berman et al. 2013) and the Yasawa islands of Fiji (Ward and Beggs 2007).

Aside from impacts to other ant species, yellow crazy ants reduce the diversity of other insects and invertebrates. Although there have been few studies on native taxa in the region, Hawaiian yellow-faced bees (*Hylaeus anthracinus*), a native species that is in decline, was not found when yellow crazy ants were present (Plentovich et al. 2021). Also in Hawai'i, *Tetragnatha* spiders were excluded by the ants, which could lead to the severe decline or possible local extinction of the spiders (Gillespie and Reimer 1993). In Tokelau, hermit crabs were excluded from areas occupied by yellow crazy ants on Nukunonu Atoll, but not killed (McNatty et al. 2009), although villagers reported the ants killing coconut crabs on Atafu Atoll (Gruber et al. 2018). On Nu'utele Island, Samoa, hermit crab numbers were lower in abundance when yellow crazy ants were present (Hoffmann et al. 2014). In Hawai'i, a decrease in the abundance of native riparian insects coincided with the arrival of yellow crazy ants in the 1970's (Hardy 1979). Aljian (2022) found that the ants did not affect the distribution of Hawaiian ghost crabs (*Ocypode* spp.). However, the study did not report the abundance of the ants, which might have been below a threshold for measurable impacts, as found elsewhere (Boland et al. 2011), and ghost crabs are known to be excluded by yellow crazy ants in the Seychelles (Gerlach 2004). The highest recorded ecological impact of yellow crazy ants is on Christmas Island, where they were estimated to have killed 10-15 million Christmas Island red land crabs between the late 1990s and early 2000s. The ants kill the crabs by spraying formic acid over sensitive areas (e.g., eyes and mouthparts), which leads to crab death when the ants are in high numbers (O'Dowd et al. 2003). If not for intensive, ongoing control programs targeting the ants, the red land crabs would likely be extinct (O'Dowd et al. 2003, Boland et al. 2011).

One of the most at-risk invertebrate groups could be native land snails. Outside the Pacific islands region, yellow crazy ants prey on or actively exclude native mollusks, reducing their abundance (Kaiser-Bunbury et al. 2014). Although there is no direct evidence from the Pacific islands region, other ant species have caused land snail declines in the region (Brook 2010). Threatened snail populations are being translocated back to French Polynesia, where they will face potential yellow crazy ant impacts.

Invasive mollusks could indirectly benefit from the presence of yellow crazy ants. For example, the mutualism between scale insects and the ants on Christmas Island led to an increase in giant African snail (*Achatina fulica*) numbers, which were previously being preyed on by land crabs (Green et al. 2011). Giant African snails are already found in many countries and territories in the Pacific islands region, and pose a health risk as they carry rat lungworm (*Angiostrongylus cantonensis*), a cause of eosinophilic meningitis in people (Cowie 2013).

Mammals also suffer when yellow crazy ant abundances are high. The yellow crazy ant was considered to be one of several factors that led to the decline and extinction of the Christmas Island shrew, *Crocidura trichura* (Meek 2000) and the Christmas Island pipistrelle (*Pipistrellus murayi*), (Lumsden et al. 2007). Christmas Island's last remaining native mammal, the Christmas Island flying-fox, *Pteropus natalis* is also threatened by yellow crazy ants (Dorrestein et al. 2019). In the presence of the ants, flying-foxes exhibit more avoidance behaviors, such as swatting and grooming, indicating they are being disturbed by the ants. However, they do not move to new roosting sites (Dorrestein et al. 2019).

Countries in the region with many endemic mammals, such as the Solomon Islands, Vanuatu, and Papua New Guinea, would seem to be at risk of yellow crazy ant impacts. But the ant has been in Papua New Guinea since the nineteenth century, and in Vanuatu for nearly 100 years, with no decline in mammal populations or species reported.

Although yellow crazy ants reduce reptile numbers elsewhere (Feare 1999, Gerlach 2004, Lach et al. 2022), impacts in the Pacific region have not been quantified beyond anecdotal reports (Gruber et al. 2018). A critically endangered gecko, tepukapili (*Lepidodactylus tepukapili*) in Tuvalu (Zug et al. 2003), is now possibly limited to two islets as one islet has washed away (S. Panapa, personal communication). One of these islets is Tepuka, which has very high abundances of yellow crazy ants (average card count of 45, with point counts as high as 93, Gruber and Panapa, unpublished data). Visually the islet is swarming with ants, and it seems likely the tepukapili is severely affected. Surveys are needed to quantify the impact of the ants, and/or translocate the gecko. These efforts are

hindered by difficult logistics and lack of funding for this work in Tuvalu. In other remote islands, it is likely that such impacts are common but undetected.

Ground- and tree-nesting birds are also vulnerable to yellow crazy ants, as the ants forage on the ground and in trees. Reports in the region and elsewhere include changed nesting behavior, reduced nesting success and injury and mortality of newly hatched chicks. Wetterer (2002) refers to a Lonely Planet report (Swaney 1994), that on Niuafo'ou in Tonga's Niua island group, yellow crazy ants attacked newly hatched chicks of the endemic and threatened ground-nesting forest bird, the Niuafo'ou megapode (*Megapodius pritchardii*).

Seabirds are a key member of island ecosystems and are particularly vulnerable to yellow crazy ants. In Atafu, Tokelau, the ants reduced the nesting success of white terns but were not observed to attack chicks (Gruber et al. 2018). Removal of African big-headed ants from Mokuauia off the coast of O'ahu led to an increase in yellow crazy ant numbers, which had worse impacts on seabirds, including Cory's shearwaters (*Calonectris diomedea*) and Audubon's shearwaters (*Puffinis iherminieri*), than the eradicated ant (Plentovich et al. 2011). In an extreme case in Kāne'ohe Bay, O'ahu, yellow crazy ants reduced nesting success of wedge-tailed shearwaters (*Ardenna pacifica*), and also maimed the shearwater chicks, blinding them and deforming their bills with formic acid (Plentovich et al. 2018). Similarly, on Johnston Atoll, the ants blinded red-tailed tropicbirds (*Phaethon rubricauda*) and reduced their nesting by 90% (Kropidlowski 2014). As concluded by Plentovich et al. (2018) "yellow crazy ants constitute a significant, and likely underestimated, risk to ground-nesting seabirds", and impacts on remote islands may not be observed, reported, or assessed. In developing countries and territories in the region, where more critical priorities demand attention, these risks are particularly difficult to manage.

Unanticipated impacts might also be observed when species other than ants are removed. Rat eradications are increasingly frequent in the region, with positive impacts on seabird numbers and their flow-on benefits. Elsewhere, rat eradications have been followed by increases in yellow crazy ant numbers, to the extent they replaced rats as the major threat (Feare 1999). The same phenomenon occurred in South Tuamotu Islands in French Polynesia after a 2015 rat eradication (T. Ghestemme, personal communication). The potential for such unexpected impacts should be considered when planning rat eradication efforts where yellow crazy ants are present.

The risk to seabird populations cannot be overstated. Seabirds have many positive effects on terrestrial and reef ecosystems. Seabird-derived nutrient inputs enhance coral growth (Lorrain et al. 2017), increase fish biomass (Graham et al. 2018), and support the reef food network from plankton

to large species like manta rays (McCauley et al. 2012). On land their nutrient inputs influence plant biomass, diversity, and community composition to the extent they are considered ecosystem engineers (Ellis 2005), and they can modify El Niño effects on plant growth (Molina-Montenegro et al. 2013). Therefore, negative impacts on seabird populations also harm terrestrial and reef productivity, with flow-on effects to artisanal fisheries, food security, and cultural values.

<Figure 5>

Agricultural Impacts

Yellow crazy ants inhabit a variety of agricultural crops, including cinnamon, citrus, coffee, cocoa, coconut, mango, sugarcane, and banana in plantations, and subsistence garden plots (e.g., Van der Goot 1916, Entwistle 1972, Nelson and Taniguchi 2012, Gruber et al. 2018). As well as directly harming plants through feeding on plant carbohydrate resources, and indirectly through mutualisms with honeydew producing plant pests, ants nesting below ground can disturb the base of plants, causing them to topple, and increase plant disease vulnerability (Feare 1999). However, the ant can also control crop pests in plantations.

Most agricultural impacts in the region have been reported from Hawai'i. There, yellow crazy ant formic acid secretions result in collateral damage to bananas. Although cosmetic, affected fruits are destroyed by commercial farmers, and sold for less at local markets (Nelson and Taniguchi 2012). In coffee plantations the ants were associated with outbreaks of green scale (*Coccus viridis*), reducing fruit production and promoting the growth of sooty mold (Ascomycete fungi), sometimes leading to tree death (Reimer et al. 1990). In Tokelau the ants affect subsistence gardening (Gruber et al. 2018). Mutualism with scale insects on coconut has been reported in New Guinea, which can affect fruit production (Young 1996). Ant-plant mutualisms are likely to impact a range of crops throughout the region, depending on the abundance of the ants and the nature of the pests.

Newly hatched free-range poultry chicks are often attacked by the ants in the Pacific. But other reports of impacts on livestock are rare in the region. In Tokelau, pig fodder was eaten, livestock were irritated, and newly hatched chickens were killed by yellow crazy ants (Gruber et al. 2013, Gruber et al. 2018).

Health and Wellbeing Impacts

When they are at low abundance, people consider yellow crazy ants to be a minor nuisance, or not a concern (Gruber et al. 2018). However, at higher abundances or when people interact with their nests, their formic acid can cause skin and eye irritations. In Australia, a farmer and his dogs were

blinded for over a week by yellow crazy ants (Lach and Hoskin 2015). In Tokelau, people reported that the ants would eat food they left out, infest outdoor cooking areas, and crawl all over people, so that they could no longer sleep outside, which had previously been enjoyed (Gruber et al. 2018). In Tuvalu, people on the remote islands of Nui, Nanumanga and Nukufetau reported the ants came into their homes, got into food left inside and outside, and crawled on people while they were sleeping, which disturbed them greatly (Gruber 2024).

Perceived Benefits

Yellow crazy ant has been effectively used as a biological control agent in agricultural systems. In Papua New Guinea, yellow crazy ants limit cacao pod weevil, *Pantorhytes biplagiatus* (Baker 1972), mirid bugs *Helopeltis* spp. (Entwistle 1972, in Holway et al. 2002), and ant species that spread the fungus *Phytophthora palmivora* (McGregor and Moxon 1985). However, these benefits can also come at a cost, with declines of native ant diversity observed in cacao plantations (Bos et al. 2008). Also in Papua New Guinea, the ant limited numbers of Araucaria looper (*Millonia isodoxa*), a pest of hoop pines (Wylie 1974). Yellow crazy ant also limited the coconut bug (*Amblypelta cocophaga*) in the Solomon Islands (Brown 1959), although its effectiveness is not consistent (Macfarlane 2024).

Perspectives on the relative benefits and harm of the yellow crazy ant are likely to depend on context. On balance, we suggest the risks outweigh the marginal benefits of the ant as biological control, and its introduction to new locales should be avoided whenever possible.

GEOGRAPHIC DISTRIBUTION IN THE PACIFIC REGION

The native range of yellow crazy ant is unconfirmed, although it is likely southeast Asia. The earliest record in the Pacific islands region is from Samoa in 1867, not long after the first record of the species, in 1851 from India. As the ant has an almost continuous distribution from Southeast Asia to eastern Polynesia, it was thought to be native to the Indian Ocean islands, parts of Micronesia and Polynesia, perhaps as far east as Tuvalu, Samoa, and Tonga (Wetterer 2005).

Going further back in time, Europe might have acted as a land bridge for the ants (or their ancestors) from Africa to Asia in the early Holocene, circa 6,000yr bp (Chen 2008). Any common ancestors between it and other *Anoplolepis* must have gone extinct in the meantime (presumably in the little ice age between 1200 and 1700 B.C.E.), and it must have made this transition outside the last ice age 18,000yr bp. As the genus *Anoplolepis* dates to > 50 million yr bp (Moreau et al. 2006), there have been many changes in distribution, and species would have evolved and disappeared. Most of

the ant's range has been sampled for genetic analysis, apart from India (H. Feldhaar, personal communication), which has been suggested as the origin. Wetterer (2005) has a comprehensive discussion on the debate over the origin of yellow crazy ant.

Based on available evidence, the yellow crazy ant's native range is likely to include India, Singapore, Indonesia, Malaysia, China, Sri Lanka, Myanmar, the Philippines, Vietnam, Cambodia, Thailand, and Brunei (Wetterer 2005), and potentially countries bordering the western Pacific, such as Taiwan, and the Ryukyu Islands in Japan (Wetterer 2005). To the east, the introduced range includes Chile and Mexico (Wetterer 2005).

Yellow crazy ants are now found in almost all countries and territories in the tropical Pacific islands region (Table 2), and potentially remain absent only from the most remote islands (Figure 6). The ants were not observed recently on Santa Cruz or Bartolomé in the Galapagos, but extensive searches were not undertaken (P. Lester, personal communication), and they could be at densities below detectability. The ant has not reached Pitcairn or Henderson in the Pitcairn Islands (Wilson and Taylor 1967, Ward 2007) and is likely to also be absent from Ducie and Oeno (D. Kinchin-Smith and C. Harrison personal communication). In the Line Islands, the ant is absent from Teraina, Kiribati (Pierce et al. 2019), and Palmyra (Handler et al. 2007). To the north, the ant is now absent from Johnston Atoll (Peck et al. 2017). Further west, in Kiribati it is potentially absent or present at very low numbers on South Tarawa, Gilbert Islands (Gruber, observations 2014-2019), and the Phoenix Islands (R. Pierce, personal communication). The ant is also absent from Rose Atoll (Peck et al. 2014), and Swains Island in American Samoa (M. Schmaedick, personal communication).

<> Table 2<>

Wetterer (2007) found no records for Nauru, Clipperton, or the Revillagigedos. The ant has since been found in Nauru, but could still be absent from Rapa Nui, Banaba (Ocean Island), and remote islands within countries and territories it is currently found. The presence or absence of the ant in many islands around French Polynesia and Micronesia is not reported.

The highest latitude the ants have been recorded at are 36.9°S (Auckland, New Zealand), but they were eradicated before cold weather in winter, which they might not have tolerated (Pascoe 2002), so this record is not a good indicator of their range (Wetterer 2005). The ants have been found occasionally at latitudes between 27.5°S and 26.9°N (Wetterer 2005), and are found in Iwo Jima (24.7°N), Okinawa (26.6°N), and mainland Japan (28.3°N), as well as Taiwan (24.9°N). In the

Pacific islands region, their distribution is currently between 23°S (New Caledonia/ Gambier and Austral Islands) and 24.7°N (Iwo Jima, Figure 6).

<> Figure 6<>

HABITAT AND CLIMATIC REQUIREMENTS

The yellow crazy ant is a lowland, tropical rainforest species (Wetterer 2005), but also inhabits mesic and dry forests in Hawai'i (Gillespie and Reimer 1993). Although not usually found in arid regions (Wetterer 2005), it can tolerate drought conditions in the Pacific islands region (e.g., Tokelau in 2011, Burne and Gruber observations; Tuvalu in 2023, S. Panapa, personal communication).

Outside the region the ant is not found in primary forest (Mezger and Pfeiffer 2011, Konopik et al. 2014). Most often it is found in environments that experience disturbance, whether natural, like the crabs on Christmas Island, which create open space by feeding on seedlings and leaf litter (O'Dowd et al. 2003), and fire regimes in northern Australia (Hoffmann and Saul 2010), or anthropogenic, such as plantations (Konopik et al. 2014), and around people's homes in the Pacific (e.g., Lester and Tavite 2004, Gruber et al. 2018).

Yellow crazy ant activity is limited by soil temperature (Way 1953). Outside the Pacific islands region, they were most active between 25 and 30°C ground temperature (Haines and Haines 1978a, Chong and Lee 2009), ceasing activity above 44°C ground temperature (Haines and Haines 1978a). Yellow crazy ants are limited by temperature at higher elevations in Hawai'i. Previously they were thought to be limited to under 600 m (Fluker and Beardsley 1970), or 1200 m ASL (Wetterer 2005). However, on Mauna Loa, they were found between 1200 m and 1275 m ASL (Peck et al. 2013).

Ecological modeling predicts that the ant's suitable range could extend to between 43°N and 46°S in 2050 (Chen 2008), and climate suitability for the ant in the region is likely to be unaffected by climate change (Bertelsmeier et al. 2015), although they will likely reach higher elevations. Although the scale of modeling in these studies provides poor resolution for individual Pacific island countries and territories, all are likely to be within the range suitable for the ant (Figure 6). Yellow crazy ant populations could be limited if future ground temperatures regularly exceed 40°C.

PHYSIOLOGY AND BEHAVIOR

Sophisticated communication among colony members is a feature among ants, which mostly use chemosensation and pheromones to modulate a variety of tasks, such as foraging, identification of

colony members and outsiders, alarm signaling, recruitment of others to tasks, and settling disputes (Wilson 1990).

Although yellow crazy ants sometimes follow trails when foraging, they often do not (Haines and Haines 1978a, Abbott 2005, authors' observations). In Tokelau, food was discovered rapidly – more rapidly than by black crazy ants, *Paratrechina longicornis* (Lester and Tavite 2004), which is a major competitor there (authors and colleagues, unpublished data) – indicating effective communication even without following trails.

Yellow crazy ant has complex, distinct pheromone signals, which might contribute to its ecological dominance (Lizon à l'Allemand and Witte 2010), and its communication could be more sophisticated than that of ants that lay down chemical trails. Disruption of communication through mimicry of pheromones has been trialed for the control of other ant species (Westermann et al. 2016), and this mechanism is a promising avenue for further investigation to control yellow crazy ants.

Inter- and intra-specific aggression moderate interactions among ant communities. Many invasive ants show no intra-specific aggression over large geographical scales. The lack of aggression in these ant species is typically associated with close genetic relatedness (or genetic distance). Aggression among yellow crazy ant colonies is positively correlated with genetic distance among nests and with dissimilarity of cuticular hydrocarbon profiles, which modulate communication (Drescher et al. 2010). This lack of aggression in turn increases their competitiveness and enables them to reach high densities and ecological dominance. Other key biological features that contribute to the dominance of invasive ants are many queens per nest (polygyny), and many nests per colony (polydomy). This combination of features leads to the formation of large, unicolonial populations, or supercolonies (Holway et al. 2002).

These features typically have a genetic component, as is the case for yellow crazy ants (Drescher et al. 2007, Drescher et al. 2010, Gruber et al. 2012, Gruber et al. 2013), and the arrival of new genotypes can change population dynamics. For example, in Tokelau, the introduction of a new genotype to Nukunonu Atoll dominated the ant community in high numbers when first assessed (Abbott et al. 2007). The influence of this genotype decreased over time, and a third genotype introduced later (Gruber et al. 2013) spread to new islets and rapidly increased in numbers (C. Perez, personal communication).

Yellow crazy ants often displace other ant species where they are abundant, or form competitive hierarchies. Examples from the region include mutual exclusion among Argentine ants, African big-headed ants, and yellow crazy ants in Hawai'i (Fluker and Beardsley 1970), and yellow crazy ants dominating seabird colonies only after African big-headed ants were removed (Plentovich et al. 2011). In Tokelau, yellow crazy ants at high abundance coexisted with 50% fewer other ant species than at low abundance on Nukunonu Atoll (Abbott et al. 2007). These observations support the idea that competitive regulation might explain why yellow crazy ant population outbreaks are relatively infrequent. Like the concept of alternate stable states, some sort of disturbance, whether environmental, the removal of other ant species or rats, or the addition of plant pests, may give yellow crazy ants a competitive edge that enables them to monopolize resources and reach high abundances. Reducing yellow crazy ant numbers might restore the competitive balance, even if that is among other invasive species, which is preferable if those species are less harmful (authors and colleagues, unpublished data).

REPRODUCTION AND POPULATION DYNAMICS

Ant reproductive systems are complex and diverse, and unusual reproductive systems are found in several invasive ants, which has been cited as one of the reasons for their ecological success. We see clonal production of queens and males in little fire ants (Fournier et al. 2005), Argentine ant workers transforming into queens (Passera et al. 1988), and a ‘green beard’ gene that modulates behavior and colony structure in red imported fire ants (Keller and Ross 1998). Yellow crazy ants could be the most unusual of all, with both reproduction by workers (Lee et al. 2017), and obligate male chimerism, which has not been found in any other animal species (Darras et al. 2023).

Reproduction is typically undertaken by queens in ant societies, and reproduction by workers is relatively unusual. However, workers of many species of ant retain their reproductive physiology. Yellow crazy ant queens produce workers, males and other queens. Yellow crazy ant workers have ovaries, but no spermathecae (i.e., they cannot be inseminated) and the *trophic eggs* that they produce are used as food primarily for queens, while their reproductive eggs develop into fertile males (Lee et al. 2017). These males carry only one set of chromosomes, whereas males produced by queens are genetic mosaics, and result from two different haploid lineages combined in the same individual (Darras et al. 2023). Whether and how these characteristics contribute to the ant’s ecological success remains to be understood.

New yellow crazy ant nests are founded through budding, where an inseminated queen or queens separate from the existing nest by walking to a new location. The queen(s) may be alone (Ito et al.

2016) or accompanied by workers (O'Dowd et al. 1999). This budding process can lead to high densities, with many nests and up to 20 million ants per hectare (Abbott 2005). Ants can also spread through mating flights, where winged queens fly to new areas. This can lead to rapid spread, and these flights have been observed in yellow crazy ants (Abbott 2006), which can spread >1,000 m per year (O'Dowd et al. 1999). It is thought that yellow crazy ants could switch between modes of colony founding in response to environmental conditions (Abbott 2006). Mating flights could be a mechanism by which yellow crazy ants spread among islets in atolls.

Nest densities and sizes, and colony sizes (many nests of related ants within an area) are variable, and have not been studied extensively. In the Seychelles nest densities approached 700 per ha (0.07 per m^2), 10 million foragers per ha (1,000 m^2) and an average of 4,000 workers and up to 36,000 workers, 40 queens and 50 males per nest (Haines and Haines 1978a). In Samoa, nest density ranged from 2.2 to 4.4 per m^2 (Hoffmann et al. 2014), while on Christmas Island the ant reached densities of up to 2,254 foragers per m^2, and nest entrance densities of 10.5 per m^2 (Abbott 2005).

Few studies have investigated variation in the life cycle of the yellow crazy ant, which has been estimated to range from 54 to 74 days in Hawai'i (Fluker and Beardsley 1970), with egg development in 18–20 days, worker larvae in 16–20 days, worker pupae in 20 days, and queen pupae in 30–34 days (Van der Goot 1916). One study estimated that workers live for six months and queens for several years, producing as few as 700 eggs annually (Dammerman 1929), although this was in the supposed native range.

Reproductive timing at the beginning of the wet season in the Pacific (Solomon Islands, Greenslade 1971b, Papua New Guinea, Baker 1976) is the same as typically found elsewhere (Van der Goot 1916, Haines and Haines 1978a, Rao and Veeresh 1991, Abbott et al. 2014). However, sometimes reproduction can commence later in the wet season in the region (Samoa, Hoffmann et al. 2014). Understanding this timing is important for management, as effective control relies on an absence of queen pupae.

Yellow crazy ants are known for their ‘boom and bust’ population dynamics (Abbott 2006, Gruber et al. 2013, Cooling and Hoffmann 2015, Lester and Gruber 2016). Often outbreaks will be overlooked, unless people report or record them. For example, during a 12-month span in 2023-2024, several outbreaks were reported on remote islands in the region, including Lobikaere and Calanin Atolls in the Marshall Islands (P. Jacques, personal communication), many of the outer islands of Tuvalu (Tuvalu Ministry of Agriculture staff, personal communication), patches of Tofua Island, Tonga, and Alofi Island, Wallis and Futuna (R. Griffiths, personal communication), newly

infested islets in Atafu, Tokelau (C. Perez, personal communication), and Fogafale islet in Funafuti, Tuvalu (Halling 2023). These outbreaks have not been quantified using card counts (the standard measure), but are based on subjective assessments of numbers, which are high enough for the reporters to be concerned.

The mechanisms driving these outbreaks are not clear, and it is likely that several factors interact. Of course, mutualisms with plant pests can play an important role, enabling the ants to dominate persistently (O'Dowd et al. 2003, Abbott 2006). Unique reproductive characteristics might make them better than other ants at establishing beachhead populations (Lee et al. 2017, Darras et al. 2023). Competitive hierarchies are also likely to regulate their populations (e.g., Fluker and Beardsley 1970, Plentovich et al. 2011), and control attempts could either reset the hierarchy (authors and colleagues, unpublished data), or result in rebounds (Lester and Gruber 2016, Plentovich et al. 2018, S. Panapa, personal communication). Several studies have found that newly arriving populations outcompete resident populations, resulting in higher prevalence and greater impacts (Abbott et al. 2007, Gruber et al. 2013 [both Nukunonu, Tokelau], Vave 2024a, b, c [all Tuvalu]).

Yellow crazy ant population numbers vary in abundance over time, and previously abundant populations sometimes experience unexpected declines or collapses (e.g., Haines and Haines 1978b, Abbott 2006, Gruber et al. 2013, Cooling and Hoffmann 2015, Lester and Gruber 2016). The mechanisms for these collapses are not known. Pathogens have been suggested, although evidence to date is inconclusive (Cooling et al. 2018). Another potential mechanism for declines could be the loss of endosymbionts, which ants sometimes use to ‘upgrade’ their nutrition, gaining valuable amino acids otherwise unavailable to them (Feldhaar et al. 2007). If these endosymbionts have a large effect on population dynamics, their loss could also result in population declines (Russell et al. 2009). Yellow crazy ants carry a range of potentially mutualistic endosymbionts including *Rhizobiales* (Sebastien et al. 2012), *Enterococcus*, *Fructobacillus*, *Gluconobacter* and *Lactobacillus* (Cooling et al. 2017), but their impact on population dynamics has not been evaluated.

RESPONSE TO MANAGEMENT

The most effective means of managing invasive species is preventing their arrival, establishment and spread. Failing that, options to directly control yellow crazy ants are typically limited to specialized pesticides, whose specificity and efficacy is continually being improved. Indirect control of plant pests is also needed when these are driving yellow crazy ant abundance. Techniques that

offer ongoing population regulation, such as RNAi, gene drives, and using naturally occurring viruses, are promising but far from operational.

Biosecurity

The most efficient biosecurity approach is to secure the pathways that move species around; that is, put in place measures to reduce the risk of invasive species being transported. The primary pathways for ants are potted plants, soils, vehicles, and machinery. The movement of plants and soils should ideally be restricted, or limited to cuttings, seeds, and germplasm.

Construction materials are a major pathway for invasive ants, and ideally Environmental Impact Assessment for development projects should include the risk of yellow crazy ants being moved domestically to islands they have not yet reached.

Border inspections of goods, machinery, and equipment are not sufficient on their own to prevent the ant's arrival. Approaches like prophylactic chemical treatment at ports, on sea containers, and on imported goods prior to leaving the exporting country, are very effective (Ashcroft et al. 2008).

Several plans outline biosecurity approaches for ants in the region (Vanderwoude et al. 2021, Hoffmann et al. 2024), and the Secretariat of the Pacific Region Environment Program (SPREP) can provide practical advice on biosecurity actions through their Protect our Islands program.

Chemical Control

Direct Control: Ants

With a few exceptions in specific cases (such as direct nest injection or drenching with chemicals (Drees and Gold 2003) or hot water (King 2024)), most ants are not effectively controlled via direct chemical application, or broadcast chemical sprays, which are sometimes recommended by pest controllers. Rather, chemical control employs the ants themselves as tools to deploy slower acting pesticides, typically using a treatment product with a toxic chemical embedded in an attractive food matrix. These products can be formulated as gels, residual sprays, granules for broadcast distribution, or hydrogels (polyacrylamide crystals)(Gruber et al. 2025).

To eradicate all the ants in a nest, colony or area, all the queens must be killed. Polygyny can make eradication attempts particularly difficult, as a nest or colony can have many queens in a relatively small area. As queens do not forage outside the nest, ant control methods use workers to take the treatment product containing toxins (commonly called 'bait') back to the queen and other workers in the nest. Worker ants feed the queen, and other members of the colony, by trophallaxis (sharing of

regurgitated food). This mechanism imposes several requirements on bait formulation: 1) it must be more attractive to the target species than alternative food sources; 2) it must be able to be shared among the colony; and 3) the ants must consume it at a rate high enough to be shared with the colony before foragers feel the effects of the toxin (e.g., Stanley and Robinson 2007).

A variety of pesticides have been used to control yellow crazy ants. Commonly used toxins to kill ants include neurotoxins (e.g., fipronil, indoxacarb, thiamethoxam, dinotefuran, imidacloprid) and stomach poisons (e.g., hydramethylnon and boric acid). Boric acid is considered to be a non-toxic or less toxic option (e.g., Kafle et al. 2020), however it can be toxic to mammals in larger doses (Kiesche-Nesselrodt and Hooser 1990). Bait stations are generally thought to be unreliable relative to broadcast baiting. Stations with Antoff® (fipronil 0.001%) on Kiritimati in Kiribati (Burne and Gruber, unpublished data), and Atafu in Tokelau (authors and colleagues, unpublished data), attracted no ants.

None of these toxins are yellow-crazy ant specific, so other invertebrates, and possibly vertebrates, which ingest the bait will also be killed. However, there have been no records of unintentional eradications of these non-target species, or other ant species. Non-target populations typically recover as the greater impact is from yellow crazy ants rather than treatment (e.g., Lach et al. 2022).

Insect growth regulators (IGRs) are also used to control ants. These slowly influence the ants' development, weakening and eventually leading to the demise of the colony. The most used IGRs are juvenile hormone mimics (e.g., (S)-methoprene, fenoxycarb, and pyriproxyfen), which prevent the ants from reaching adulthood. Insect growth regulators are sometimes chosen as they are considered less environmentally harmful. However, if other invertebrates, including crabs, consume them, IGRs can have impacts on their populations (Linton et al. 2009). They can be used together with other toxins. In Australia combinations of DistancePlus® (pyriproxyfen 0.5%) and Antoff® have successfully controlled yellow crazy ants in the short term (Webb and Hoffmann 2013).

The success of programs to control yellow crazy ants in the region has been mixed, and there has been only one verified eradication, on Johnston Atoll, where efforts began in 2010, and eradication was declared in 2021 after much effort (Vicente 2021). Several commercial products tested were not effective, and Antoff ® could not be used because of regulatory restrictions (Kropidlowski 2014). The program used a combination of hydrogels saturated with a sucrose solution, either alone or sequentially with a cat food bait, both of which contained dinotefuran (Peck et al. 2017).

On O'ahu, Plentovich et al. (2018) used Maxforce Complete (hydramethylnon 1.0%) and Provaunt (indoxacarb 10-30%) in a matrix of dark karo syrup and xanthan gum, to control yellow crazy ants in seabird colonies. Although numbers were initially dramatically reduced (Maxforce Complete 98%; Provaunt 97.6%), within three months their numbers rebounded to pre-treatment levels.

Hydrogels are becoming more popular as a delivery mechanism for ant control (e.g., Tay et al. 2017). Recently eradication was attempted in Tetiaroa in the Society Islands, French Polynesia using hydrogels containing a fipronil and sugar solution (J. DeVore and S. Ducatez, personal communication). Eradication will require long-term monitoring to confirm. The same approach is being used to eradicate yellow crazy ants on Temoe Atoll in the Gambier Islands, French Polynesia (T. Ghestemme, personal communication).

Several efforts to control yellow crazy ants using Antoff® are ongoing and/or have not been published. In French Polynesia, yellow crazy ants were controlled for conservation purposes on Fatu Hiva in the Marquesas and Manui in the Gambiers (T. Ghestemme, personal communication). On Kiritimati in Kiribati an attempt to eradicate the ant from ~1 ha, using standard Antoff® broadcast baiting appeared successful, with no detections more than two years after treatment ceased (Pierce, Gruber, Burne and Binoka, unpublished data). However, the ants were later seen in new locations, although their abundance remained low in 2024 (R. Pierce, personal communication). In Tokelau, where eradication was not the goal, treatment with Antoff® and other products in 2015 resulted in effective long-term control, with ant numbers still low in 2024, 10 years after treatment (authors and colleagues, unpublished data). In Tuvalu, control efforts on Tepuka islet were initially successful, but the populations rebounded within five years, possibly due to mutualism with scale insects, or because 10% of the islet was not treated (M. Lonalona and S. Panapa, personal communication). In Nauru the ant was controlled soon after its arrival with a single treatment of Antoff® broadcast by hand, but was not monitored (Saurara and Vaqalo 2015).

Other factors must be considered in the design of ant control or eradication projects. Reproductive phenology, which is affected by seasonality (and by diet), should ideally be known, so that treatment occurs when queen pupae are absent. As this reproduction typically occurs at the start of, or during, the wet season, timing treatment for the middle of the dry season could be sufficient in the region. However, seasons in the region are becoming increasingly unpredictable due to climate change, which would affect reproductive phenology also.

The bait must be distributed so that the ants encounter it. For ants that forage in the tree canopy, mist blowers can be used to distribute granular baits (authors and colleagues, unpublished data). Drones

are increasingly being used in hard to access areas, with helicopters used for landscape-scale treatments (Hoffmann et al. 2016). However drone baiting was not effective in 2018 on Manui, French Polynesia (T. Ghestemme, personal communication). Aerial baiting is not recommended in riparian areas as toxins can enter the waterway and poison non-target species. Non-target impacts from aerial distribution of toxic bait could potentially be higher than ground baiting if there are specific species that use the canopy. To our knowledge this has not been assessed.

Some products can have serious environmental impacts if misused or used frequently. If ants are at high numbers, they will remove all bait from the environment, but at low numbers, much bait may be left in the environment, increasing consumption by non-target invertebrates, and lagoon runoff that could affect fish and marine invertebrates. Short term impacts on other ant species were found for Distance Plus® (Webb and Hoffmann 2013), and the impacts of Engage P®, Engage+® (S)-methoprene 0.5%) and Antoff® on skinks were outweighed by the impacts of yellow crazy ants (Lach et al. 2022). On Atafu, Tokelau, treatment with Antoff® resulted in immediate negative impacts on invertebrate numbers, but no mortality was detected on lizards, birds, or crabs (authors and colleagues, unpublished data). Environmental monitoring can be difficult, and tools that can detect pesticide residues and metabolites in the field, for example using aptamer technology (Phopin and Tantimongcolwat 2020), would be useful.

Eradication requires many repeated treatments. Therefore, deciding to pursue eradication rather than a one-off control effort that can knock back the population to relatively harmless levels, requires choosing between the impacts of the ants and the potential impacts of the bait. There have been no studies on long term non-target impacts, including fipronil metabolites, which can be more toxic than fipronil itself, or possible runoff effects.

Regardless of the method, successful eradication requires effective detection methods, and ants are difficult to detect when in low numbers. On Johnston Atoll, a program of systematic monitoring (Peck et al. 2017), and detector dogs (Vicente 2021) confirmed eradication. The use of eDNA is a promising tool to detect yellow crazy ants in water and soil (Villacorta-Rath et al. 2023). These sophisticated means of detection are not available or feasible in many remote Pacific islands.

Further information on the control of yellow crazy ants and other ants, including lists of pesticides, their active ingredients and potential non-target impacts, case studies, and contacts can be found in the *Getting rid of ants* section of the Pacific Invasive Ant Toolkit (Gruber et al. 2025).

Indirect Control: Plant Pest Mutualists

Chemical methods to control plant pest mutualists are widespread but can require persistent applications. An Integrated Pest Management (IPM) approach is recommended when dealing with these pests, so that insecticides are used minimally as a knockdown when the pests are at high abundance. On Rose Atoll, where yellow crazy ants are absent, the systemic insecticide imidacloprid (product details not provided) was injected into *Pisonia* trees to eliminate *Pulvinaria* scales from their leaves, with short-term suppression observed, although scale abundances sometimes rebounded over time (Peck et al. 2014).

Biological Control

The yellow crazy ant is generally considered to have no natural enemies except other ants. However, in Borneo the giant river toad (*Phrynoidis juxtaspera*), an ant-specialist, was an effective native predator of the ant (Konopik et al. 2014).

Classical biological controls for ants have been extensively investigated for species such as red imported fire ants (e.g., Oi et al. 2015), with less work on other species, including yellow crazy ants. A few studies have investigated whether the outbreaks and collapses of yellow crazy ants (Gruber et al. 2013, Cooling and Hoffmann 2015) could be modulated by pathogens (Gruber 2012, Cooling 2015, Cooling et al. 2017). Fungi such as *Beauveria bassiana* and *Metarhizium anisopliae* are used in ant control, but *M. anisopliae* was found to have no effect on yellow crazy ants (Cooling 2015).

Metagenomic and metatranscriptomic studies have found several known and putative bacteria and viruses in yellow crazy ant populations (Gruber 2012, Sebastien et al. 2012, Cooling 2015, Cooling et al. 2017, Lee et al. 2020, Lee et al. 2022), but no links have been made to population dynamics. There is evidence that pathogens affect oocyte production in the ants, however, the cause is not known (Cooling et al. 2018). Although these types of studies could reveal biological controls for yellow crazy ants, it could take several decades before they are operational.

Another approach for the control of insects is the use of RNA interference (RNAi) or CRISPR (clustered regularly interspaced short palindromic repeats) techniques (Allen 2021), which interfere with gene regulation and function. Developing these tools is complex and requires a reliably annotated genome that can demonstrate the genetic basis of physiology and/or behavior. This is not yet available for yellow crazy ants and is complicated by their unusual reproductive system. The ant’s unique pheromone signaling system (Lizon à l'Allemand and Witte 2010) might be a potential

target for such genomic tools, if their communication could be disrupted sufficiently to limit foraging. Again, while promising, it will take many years before these tools are ready to use.

Indirect biological control

Indirect biological control of yellow crazy ant populations through their honeydew producing plant pest mutualists could be occurring naturally in the Pacific islands region, as many biological controls have been introduced for agriculture purposes. For example, *Pulvinaria urbicola* is controlled elsewhere by parasitoid wasps *Coccophagus ceroplastae*, *Euryischomyia flavithorax*, and *Metaphycus luteolus*, and by the beetle *Cryptolaemus montrouzieri*, known as the mealybug destroyer beetle or mealybug killer (Smith et al. 2004). The latter is a generalist predator, as is the beetle *Novius cardinalis* (previously known as *Rodolia cardinalis* and *Vedalia cardinalis*). They and several other scale insect biological controls such as *Cryptognatha nodiceps*, *Cryptognatha gemellata*, *Rhyzobius satelles*, and *Pseudoscymnus anomalus* are found in the region (Jackson 2023).

A parasitoid wasp, *Tachardiaephagus somervillei*, of yellow lac scale (Neumann et al. 2018) has been released as a biological control on Christmas Island. The wasp introduction has led to significant declines in yellow lac scale abundance, and reductions in yellow crazy ant activity where those scale insects were used by the ant. However, the ants are persisting in areas where other (soft) scale insects are present, and potential biological controls for those insects are being actively researched (R. Willacy, personal communication).

As an insurance policy, consideration could be given to introducing generalist biological controls in areas where potential plant pest mutualists are present, but yellow crazy ants are absent, or vice versa, subject to suitable risk assessment. A more complete list of the biological control agents released in the region would be useful also, which should ideally be held by the Secretariat of the Pacific Community (SPC).

PROGNOSIS AND RECOMMENDATIONS

Biosecurity is the most effective means of managing invasive species, by preventing their arrival, establishment, and spread. Although prevention of yellow crazy ant arrival is no longer an option in almost all countries and territories in the region, preventing the arrival and spread of their plant pest mutualists is needed (Loope and Krushelnycky 2007), particularly those with documented contributions to yellow crazy ant abundance and impacts.

Local governments, regional agencies, and funders could support improved domestic biosecurity, and international biosecurity for the few countries and territories that do not yet have yellow crazy ants. The ants might be present in many places at abundances below detection, so confirming their absence over many thousands of islands is infeasible. However, the transport routes from where the ants are known to be present could be better secured, using resources that have been developed to date.

As a form of insurance, more intensive research would be useful on the introduction of biological control insects for the honeydew producing plant pests that the yellow crazy ant forms mutualisms with. Many biological control insects have been released in the Pacific region in the past, but these do not appear to be well-documented, or records are not publicly available. Importantly, data mobilization of such records to comprehensive data sources, such as GBIF, will encourage transparency and continuity in efforts among organizations and jurisdictions.

Without better biosecurity measures and compliance, it seems likely that the yellow crazy ant will soon be ubiquitous throughout the Pacific islands region. A better understanding of the causes of population outbreaks and collapses, and how to manage them is therefore increasingly important. As eradication is likely to be feasible only in rare cases, efforts should focus on sustainably mitigating the impacts of the ants with improved control methods, and education on managing the ant. However, pesticides are likely to be used for the foreseeable future, and longer-term monitoring by researchers and practitioners is needed to better understand the ongoing impacts of pesticides and their metabolites. Better tools to detect pesticide residues and metabolites in the field, such as aptamer technology, are needed.

Eradications of other ants, and of yellow crazy ant interspecific competitors such as rats, should consider the wider ecological context during feasibility assessments, to be aware of potential unanticipated negative secondary impacts, as found by Hill et al. (2003), Plentovich et al. (2018), and T. Ghestemme, personal communication. Yellow crazy ant numbers can be simply measured using card counts, with point counts adequate if time is limited. If any plant pests are being used by yellow crazy ants, they should be controlled before, during and after any eradication efforts. The potential presence of yellow crazy ants should also be a consideration for risk assessments for translocations of threatened species as part of restoration efforts.

Small developing countries and territories are often challenged by their remoteness, small workforces, and lack of on-hand technical resources. For example, tools such as eDNA detection and detector dogs are not realistic for many countries or territories without outside support. The

New Zealand government supported a detector dog program for the Cook Islands, Tonga, Samoa and Fiji from 2018-2023, but this was limited to detection of illicit drugs. Such programs could also potentially assist with biosecurity surveillance. Recently French Polynesia initiated a border biosecurity detector dog program with the support of SPREP, the New Zealand Ministry of Primary industries, and the European Union (D. Sadler, personal communication).

Perhaps the ubiquity and long presence of yellow crazy ants on many Pacific islands has caused people to be tolerant and desensitized to their presence, so that they are considered a minor nuisance. However, yellow crazy ants have repeated, documented outbreaks that make life stressful for people, threaten agriculture, and harm native plants and animals, and deserve attention as a biosecurity risk in the Pacific islands region.

ACKNOWLEDGEMENTS

We are grateful to the series editor (Aaron Shiels) for inviting us to contribute this article to Pacific Science. Special thanks to Ray Pierce (Eco Oceania), Phil Lester (Te Herenga Waka–Victoria University of Wellington), Sam Panapa (Tuvalu Environment), Matio Lonalona and the Tuvalu Agriculture team, Uata Vave and Itaia Lausaveve (Live and Learn Tuvalu), and Tuvalu communities, Christian Perez (Tokelau Ministry of Economic Development, Natural Resources and Environment), Dominic Sadler (SPREP), Paul Jacques, Richard Griffiths, Amy Levine and Jesse Friedlander (Island Conservation), Thomas Ghestemme (Société d'Ornithologie de Polynésie Manu), Jayna DeVore and Simon Ducatez (Université de la Polynésie française), Mark Schmaedick (American Samoa Community College), Andy Schofield, Chloe Harrison, David Kinchin-Smith and staff (Royal Society for Protection of Birds), Sheldon Plentovich (United States Fish and Wildlife Service), Glenn Bellis (Charles Darwin University), Jean-Yves Hiro Meyer (Délégation à la Recherche de la Polynésie française), James Russell and Sebastian Steibl (University of Auckland), Heike Feldhaar (Universität Bayreuth), Peter Green (Latrobe University), Lori Lach (James Cook University), Rosie Willacy and Sarah Wilson (Parks Australia), and Grahame Jackson for their contributions. Grateful thanks also to Daniel Wojcik and Sanford Porter for compiling and maintaining the FORMIS Endnote library, which greatly simplified the search for sources. Finally, we acknowledge the many people who have contributed to our work on ants in the Pacific islands region since 2011. Too numerous to mention here, their names can be found on the credits page of the Pacific Invasive Ant Toolkit.

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FIGURES AND TABLES

Figure 1. Yellow crazy ant worker and queen (A), three workers (B), and two workers (C). Characteristic features of the workers include long slender bodies, long legs and antennae, and relatively large eyes. Images: Phil Lester, with permission.

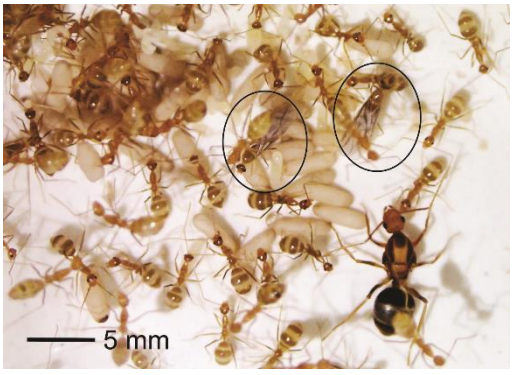

Figure 2. Yellow crazy ant queen, workers, and worker pupae. Two winged males, which are rarely seen, are circled. Note that in this image, most worker gasters have a striped appearance as they are distended. Image: Meghan Cooling.

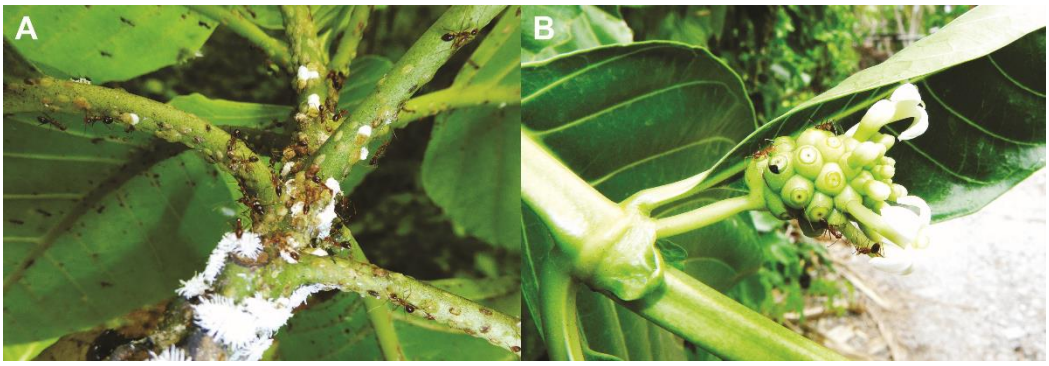

Figure 3: Yellow crazy ants tending scale insects on *Pisonia grandis*, with *Cryptolaemus montrouzieri* also present, on Motu Aie, Tetiaroa (A: Jean-Yves Hiro Meyer, with permission) and on *Morinda citrifolia* extra-floral nectaries, Atafu, Tokelau (B: Monica Gruber).

Figure 4. Yellow crazy ants scavenge and/or prey on a wide variety of vertebrates and invertebrates. A: skink (Phil Lester). B: stick insect (Monica Gruber). C: crab (Phil Lester).

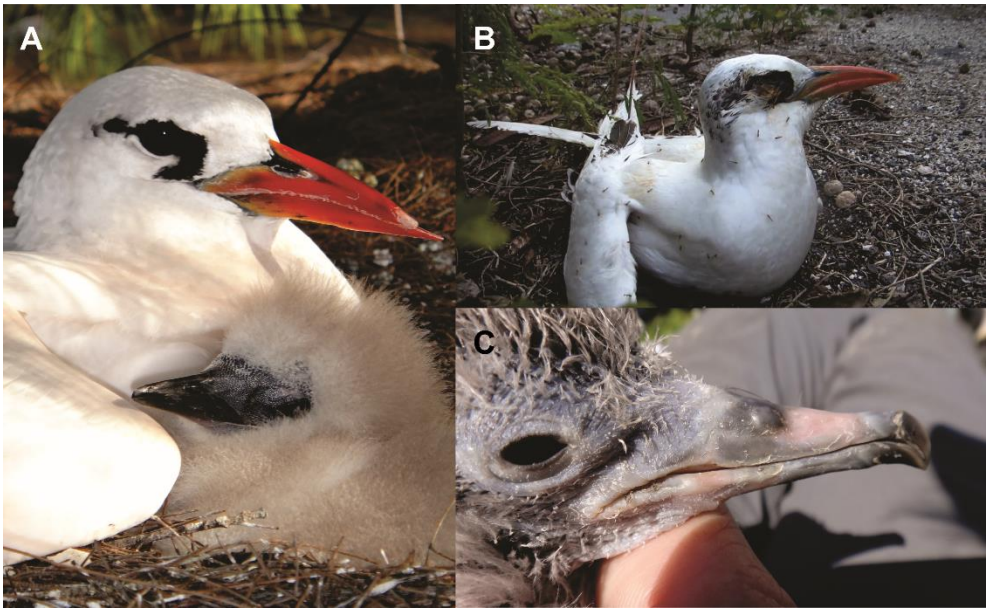

Figure 5: Normal red-tailed tropicbird adult and chick (A), adult being swarmed by yellow crazy ants (B), and chick with deformed eye and bill and loss of feathers, caused by the ants' formic acid (C).Images: Sheldon Plentovich/United States Fish and Wildlife Service, with permission.

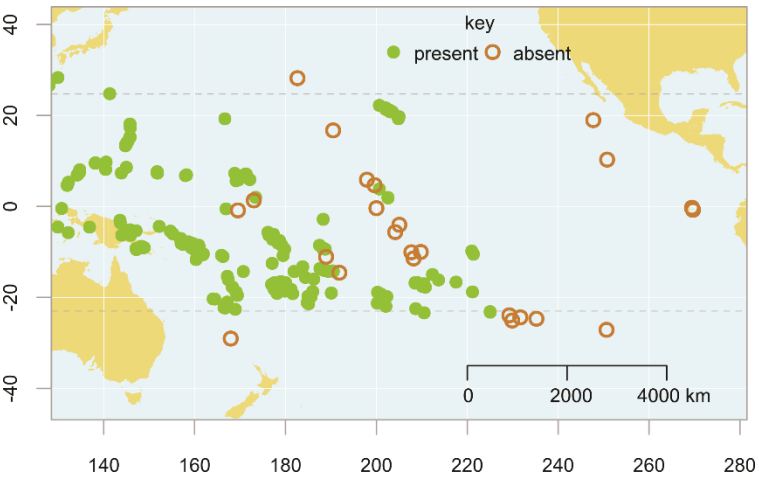

Figure 6. Map of the Pacific islands region showing locations where yellow crazy ant is confirmed to be present and confirmed to be absent. The grey dashed lines indicate the current latitudes within which yellow crazy ants are found in the Pacific islands region (23°S and 24.7°N). The upper and lower borders of the map encompass the latitudes predicted to be suitable for the ants in 2050 . The presence of the ant on many islands is not known, particularly those that are small and remote. The map was created using the R packages *rgbif* and *maps* from the data sources in Table 2. The figure does not show observations outside the tropical Pacific islands region (i.e., Northern and

Northeastern Australia, North and Central America and Japan, although Iwo Jima and the Ryukyu Islands are shown).

Table 1: Known plant pests tended by yellow crazy ants, and their (or congeners) prevalence in the region, from occurrence data in the Secretariat of the Pacific Community (SPC) Pest List Database (https://pld.lrd.spc.int/), together with potential biological control agents. * indicates the ant is reliant on the pest as a carbohydrate resource on Christmas Island, and has been associated with high yellow crazy ant abundance. ? indicates that *Cryptolaemus montrouzieri* is a generalist predator of Pseudococcidae (mealybugs) and Coccidae (soft scale insects), and has not been specifically tested on these species.

Plant pest species	**Common name**	**Pest prevalence in the region**	**Potential biological control**	**References**
Cerococcus indicus	spiny brown coccid	Congeners in Fiji and the Cook Islands	?*C. montrouzieri*	(Neumann et al. 2016)
Ceroplastes ceriferus	Indian wax scale	Seven countries/ territories	?*C. montrouzieri*	(Haines and Haines 1978b, Neumann et al. 2016, Jackson 2023)
Ceroplastes rubens	pink wax scale	14 countries/ territories	?*C. montrouzieri*	(Neumann et al. 2016)
Coccus celatus *	coffee green scale	Congeners only. See *C. hespiridum* and *C. viridis*	?*C. montrouzieri*	(O'Dowd et al. 2003, Neumann et al. 2016)
Coccus hesperidum *	brown soft scale	15 countries/ territories	?*C. montrouzieri*	(Neumann et al. 2016)
Coccus viridis	Green scale	As for *C. hesperidum*	?*C. montrouzieri*	(Haines and Haines 1978b, Reimer et al. 1990)
Dysmicoccus finitimus	Asian coconut mealybug	Congeners only in 16 countries/ territories	?*C. montrouzieri*	(Neumann et al. 2016)
Icerya purchasi	cottony cushion scale	Seven countries/ territories and congeners in two territories	*Novius cardinalis*	(Neumann et al. 2016)
Milviscutulus mangiferae	mango shield scale	Seven countries/ territories and congeners	?*C. montrouzieri*	(Neumann et al. 2016)
Nipaecoccus viridis	spherical mealybug	Five countries/ territories and congener in Samoa	?*C. montrouzieri*	(Neumann et al. 2016)

Plant pest species	Common name	Pest prevalence in the region	Potential biological control	References
Parasaissetia nigra	nigra scale	16 countries/ territories	?*C. montrouzieri*	(Neumann et al. 2016)
Pseudococcus longispinus	long-tailed mealybug	10 countries/territories and congeners in seven others	?*C. montrouzieri*	(Neumann et al. 2016)
Pulvinaria psidii	*g*reen shield scale	13 countries/ territories and congeners in nine others	?*C. montrouzieri*	(Neumann et al. 2016)
Pulvinaria urbicola	urbicola soft scale	Eight countries/ territories	*Coccophagus ceroplastae*, *Euryischomyia flavithorax*, *Metaphycus luteolus*, *C. montrouzieri*	(Neumann et al. 2016)
Saissetia coffeae *	hemispherical scale	12 countries/ territories and congeners in 15 countries/territories	?*C. montrouzieri*	(Neumann et al. 2016)
Tachardina aurantiaca *	yellow lac scale	absent	*Tachardiaephagus somervillei*	(O'Dowd et al. 2003, Neumann et al. 2016)

Table 2: Confirmed presence of *Anoplolepis gracilipes* in the ant's non-native range in the Pacific islands region, including islands within the country/territory, if known (Extent), earliest reported date and sources for that and subsequent records. The table has been derived from the distribution database described in Gruber et al. (2017), updated in September 2024, together with unpublished reports, and records from the Global Biodiversity Information Facility (GBIF 2024) accessed from R (R Core Team 2024) via *rgbif* (Chamberlain and Boettiger 2017, Chamberlain et al. 2024).

Country/territory	Extent	Date	Sources
American Samoa	Ofu, Olosega, Ta'ū, Tutuila, Aunu'u	1867	(Wilson and Taylor 1967, Wetterer and Vargo 2003, Peck and Banko 2015, M. Schmaedick, personal communication)
Cook Islands	Manuae (Akaiami and Tapuaetai), Rarotonga, Mitiaro, Aitutaki, Atiu	1937	(Wilson and Taylor 1967, GBIF 2024, Russell, Steibl and colleagues, unpublished data, for Akaiami and Tapuaetai)

Country/territory	Extent	Date	Sources
Federated States of Micronesia (FSM)	Chuuk, Pohnpei, Yap (Carolines)	1935	(Wetterer 2005)
Fiji	Kadavu, Lau, Lomaiviti, Rotuma, Vanua Levu, Viti Levu, Taveuni and Yasawa Islands (offshore islands also)	1876	(Wilson and Taylor 1967, Wetterer 2005, Ward and Wetterer 2006, Sarnat and Economo 2012)
French Polynesia	Austral, Gambier, Marquesas, Society, and Tuamotu groups	1907	(Wilson and Taylor 1967)
Guam		1911	(Wetterer 2005)
Hawai'i (United States)	Hawai'i, Kaua'i, Maui, Molokai, Lanai, and O'ahu	1950	(Wilson and Taylor 1967, Martin 2012, Peck et al. 2013)
Japan	Iwo Jima, Ryukyu Islands		(Wetterer 2005, GBIF 2024, for Iwo Jima)
Kiribati	Line Islands (Kiritimati, Tabuaeran), Gilbert Islands (Marekai and likely other atolls and islands)	1924	(Wilson and Taylor 1967, Wetterer 2005, Pierce et al. 2019, GBIF 2024, for Marekai)
Nauru		2013	(McKenna et al. 2013)
New Caledonia	Grand Terre, Loyalty Islands	1882	(Wetterer 2005)
Niuē		1965	(Collingwood and van Harten 2001, Wetterer 2005)
Commonwealth of the Northern Mariana Islands (CNMI)	Guguan, Pagan, Saipan, Rota	1911	(Wetterer 2005, Evenhuis et al. 2010)
Palau	Babeldaob, Sonsorol, Koror, Kayangel, Peleliu, Angaur	1936	(Wetterer 2005, GBIF 2024for islands within Palau)
Papua New Guinea	Central, East Sepik, Oro Provinces and East New Britain, Long Island, Madang	1896	(Wetterer 2005)
Republic of the Marshall Islands (RMI)	Ailinglaplap, Kili, Mili (Nadikdik), Majuro (Lobikaere, Calanin), Jaluit, Arno. Likely to be on other islands	1904	(Wetterer 2005, P. Jacques personal communication for Mili, Lobikaere and Calalin, GBIF 2024, for Jaluit and Arno, GISD 2024, for Ailinglaplap)
Samoa	Savai'i, Upolu, Nu'ulua, Nu'utele. Likely to be on Apolima and Manono	1867	(Wilson and Taylor 1967, Wetterer and Vargo 2003, Savage et al. 2009, Hoffmann et al. 2014)
Solomon Islands	Central Province, Choiseul, Guadalcanal, Santa Isabel, Makira, Malaita, Temotu (Santa Cruz), San Cristobal,	1916	(Wetterer 2005, GBIF 2024, for San Cristobal and Nggela)

Country/territory	Extent	Date	Sources
	Rennell, Nggela, and Western Provinces		
Tokelau	Atafu, Fakaofo and Nukunonu atolls	1934	(Wilson and Taylor 1967, Lester and Tavite 2004, Gruber et al. 2013, for Atafu)
Tonga	Ha'apai, Niua, Tongatapu, and Vava'u groups and 'Eua	1870	(Wilson and Taylor 1967, Wetterer 2002)
Tuvalu	Funafuti, Nanumanga, Nanumea, Niulakita, Niutao, Nui, Nukufetau, Nukulaelae, Vaitupu	1870	(Wilson and Taylor 1967, Wetterer 2005, Vaqalo et al. 2014, Gruber 2024)
Vanuatu	Efate, Erromango, Espiritu Santo, Malekula, Tanna. Likely on other islands	1929	(Wetterer 2005, GBIF 2024, for Espiritu Santo, Malekula and Tanna)
Wake Atoll (United States)	Wake, Wilkes and Peale islets	2007	(Peck et al. 2024)
Wallis & Futuna	Uvea (likely on islets in the Wallis group), Futuna, Alofi	1913	(Wilson and Taylor 1967, Wetterer 2005, Gruber observations for Futuna and Alofi)