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Review

Improving invasive ant eradication as a conservation tool: A review

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ABSTRACT

While invasive species eradications are at the forefront of biodiversity conservation, ant eradication failures are common. We reviewed ant eradications worldwide to assess the practice and identify knowledge gaps and challenges. We documented 316 eradication campaigns targeting 11 species, with most occurring in Australia covering small areas (<10 ha). Yellow crazy ant was targeted most frequently, while the bigheaded ant has been eradicated most often. Of the eradications with known outcomes, 144 campaigns were successful, totaling approximately 9500 ha, of which 8300 ha were from a single campaign that has since been partially re-invaded. Three active ingredients, often in combination, are most commonly used: fipronil, hydramethylnon, and juvenile hormone mimics. Active ingredient, bait, and method varied considerably with respect to species targeted, which made assessing factors of eradication success challenging. We did, however, detect effects by active ingredient, number of treatments, and method on eradication success. Implementation costs increased with treatment area, and median costs were high compared to invasive mammal eradications. Ant eradications are in a phase of increased research and development, and a logical next step for practitioners is to develop best practices. A number of research themes that seek to integrate natural history with eradication strategies and methodologies would improve the ability to eradicate ants: increasing natural history and taxonomic knowledge, increasing the efficacy of active ingredients and baits, minimizing and mitigating non-target risks, developing better tools to declare eradication success, and developing alternative eradication methodologies. Invasive ant eradications are rapidly increasing in both size and frequency, and we envisage that eradicating invasive ants will increase in focus in coming decades given the increasing dispersal and subsequent impacts.

Contents

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1. Introduction

Invasive alien species continue to impact species, ecosystems, and human welfare (Simberloff, 2013). Ants are one of the most cosmopolitan invasive taxa: dozens of species have invaded islands and continental areas around the globe (Suarez et al., 2010). Certain ant species exhibit a suite of characteristics that result in anthropophilic tendencies. Consequently, invasive ants continue to spread globally (Ascunce et al., 2011; McGlynn, 1999). These tramp species are having direct and indirect negative impacts on natural and managed ecosystems (Holway et al., 2002; Lach and Hooper-Bui, 2010). In some cases, those impacts can be complex and dramatic (O'Dowd et al., 2003). In a few cases, the biodiversity benefits of removing invasive ants have been documented (Gaigher et al., 2012; Hoffmann, 2010).

Invasive species eradications have been at the forefront of biodiversity conservation gains over the past two decades (Veitch et al., 2011). Over 1200 invasive mammal eradications have been attempted on over 800 islands worldwide (DIISE, 2014). The conservation benefits of such conservation actions are increasingly well documented (Donlan et al., 2007; Lavers et al., 2010). Despite a long history of invasive ant management, methods and approaches vary widely and eradication failures are common (Hoffmann et al., 2011a). Social insects, like invasive ants, complicate management actions due to their complex interactions with each other and the environment. For example, a caste system can prevent reproductive members of a colony from getting sufficient exposure to bait with an active ingredient that is targeted at foragers (Moller, 1996). Thus, many popular approaches to insect management (e.g., integrated pest management) are inappropriate for social insects because of a failure to expose reproductively active individuals (Gentz, 2009). These characteristics present unique challenges for eradication, or even effective control, of invasive ants (Silverman and Brightwell, 2008). However, new developments in insecticides and other active ingredients (collectively referred to hereafter as AI) and management methodologies have improved practitioners' ability to eradicate invasive ant populations (Hoffmann et al., 2011a).

Over the past decade, taxa-specific reviews of invasive species eradications have helped clarify the benefits, costs, and risks of eradication as a biodiversity conservation tool, as well as identify important research needs (Campbell et al., 2011; Howald et al., 2007; Nogales et al., 2004). Here, we review ant eradication attempts worldwide. In particular, we assess the status of ant eradication as a conservation practice and explore what factors influence success or failure. We characterize the approaches and outcomes of ant eradication campaigns, and identify knowledge gaps and challenges to be addressed by research and other activities that will likely improve the ability to safely eradicate invasive ant populations.

2. Methods

We compiled data from publications, gray literature (e.g., government reports), and personal communications on ant eradications. We only included efforts that explicitly targeted a spatially discrete ant population for eradication. For example, programs that targeted a subset of a population for eradication, which is common in efficacy trails, were not included in our review. Further, we did not include historical eradications that used organochlorine sprays because those insecticides are now widely banned, and insecticide spraying is no longer advocated in most situations for ant eradications (Hoffmann et al., 2011a). For each eradication effort, we collected information on location, species, area treated, methods used, AI, cost, and outcome. We judged failure or success based on the outcome and evidence reported by those that conducted the eradication. For the purposes of our review, an eradication attempt was considered successful if two years of monitoring occurred with no detection (FAO, 1998; Howald et al., 2007). We treated the year of the final treatment as the eradication date. In some instances, multiple attempts were made to eradicate a single population. In these cases, each attempt followed by a monitoring assessment was considered an independent eradication attempt, and all but the final attempt were counted as failures. Our unit of analysis was the area of each spatially discrete population in which eradication was attempted (referred to hereafter as a campaign), which in the case of islands is often a fraction of an island as opposed to the entire island as occurs for other invasive species eradications (e.g., rodents). Data from the Database of Islands and Invasive Species Eradications (DIISE, 2014) was accessed 10 March 2016, and we used events only for invasive mammals (excluding domestic animal populations), whole island eradications, and events that were classified as good or satisfactory data quality. For determining success rates, we considered only successful or failed projects, and excluded reinvasion as these can also include misdiagnosed operational failures. Statistical analyses were conducted using R (R Development Core Team, 2011) with an alpha-level of $p = 0.05$, and details are described below.

3. Results

3.1. The state of invasive ant eradication

The history of ant eradications began with multiple, large unsuccessful campaigns. Starting in the 1950s, the red imported fire ant program (*Solenopsis invicta*) in the southeast United States was one of the first eradication programs, and one of the largest eradication programs ever attempted for any species. For 16 years, more than 56 million hectares were treated with a myriad of liquid-based compounds (Williams et al., 2001). Eradication was not achieved. Over the same time period in Australia, programs covering tens of thousands of hectares targeted the Argentine ant (*Linepithema humile*) (Van Schagen et al., 1994). With the banning of organochlorine compounds, these programs ended without achieving eradication. When the limitations of liquid sprays were widely recognized, practitioners developed solid granular baits (Lofgren et al., 1975; Williams et al., 2001). While these bait developments improved invasive ant management, large campaigns initiated in the 2000s in China and Australia continue to struggle to achieve eradication (Vanderwoude et al., 2003; Zhang et al., 2007).

Overall, we documented 316 eradication campaigns targeting 11 ant species (Fig. 1). Most campaigns have occurred on continents ($n = 236$, 75%). Slightly less than half of all campaigns were successful ($n = 144$), and the remaining were either failures (74) or of unknown outcome (98), with 92 of the latter being in progress (Fig. 2). Over 50% of the campaigns were unpublished (Supplementary Materials). Most successful eradications were in Australia and targeted an area less than 10 ha (Fig. 3). The total area that invasive ants have been eradicated from worldwide is approximately 9500 ha (Fig. 2).

We identified only five successful eradications prior to 2000, totaling 7 ha (Fig. 2). These campaigns targeted yellow crazy ant (*Anoplolepis gracilipes*) from a small area of unknown size on Praslin Island

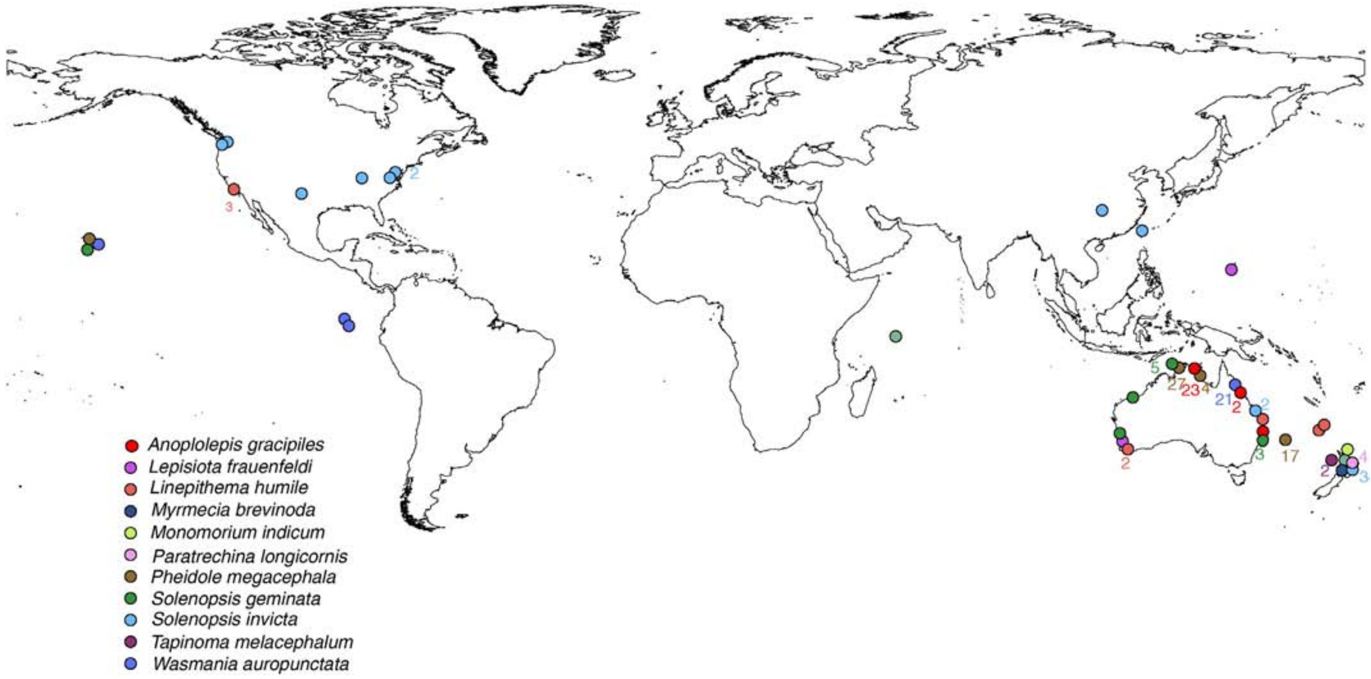

Fig. 1. The global distribution of invasive ant eradication campaigns. We documented 316 campaigns targeting 11 species. Specific details of the eradication campaigns are provided in Supplementary Materials.

(Seychelles), red imported fire ant from 3 ha in the United States, little fire ant (*Wasmannia auropunctata*) from 2 ha on Santa Fe Island (Galapagos), Argentine ant from 1 ha in Perth (Australia), and a few nests of bulldog ant (*Myrmecia brevinoda*) in New Zealand (Abedrabbo, 1994; Haines and Haines, 1978; Hoffmann et al., 2011a; Lester and Keall, 2005; Thorvilson et al., 1992). A notable success in the early 2000s was the eradication of the little fire ant from Marchena Island (Galapagos, 22 ha) (Causton et al., 2005). By the mid-2000s, five eradications greater than 10 ha were successfully conducted: yellow crazy ant in northeast Arnhem Island (Australia, 10 ha and 15 ha), red imported fire ant from a location in Taiwan (11 ha) and Dayongqiao Park (China, 20 ha,), Argentine ant from Brisbane (Australia, 41 ha), and red imported fire ant from Yarwun (Australia, 71 ha) (Yijuan Xu, personal communication; Hoffmann et al., 2011a; Hoffmann, 2011; Hwang, 2009).

With respect to area, the largest successful eradication to date also took place in the mid-2000s: the eradication of red imported fire ant from the port of Brisbane (Australia) (Wylie et al., 2016). The program treated a population covering 8300 ha, using multiple methods—aerial broadcast, hand broadcast, and nest drenching. This represents approximately 85% of the global area that ants have been eradicated (Fig. 2). Multiple AIs were used (i.e., fipronil, hydramethylnon, methoprene, and pyriproxyfen) (Wylie et al., 2016). The program targeted a genetically distinct population that was approximately 20 km from another larger infestation throughout Brisbane (>20,000 ha). Since the eradication, the larger population has invaded some of the area that was

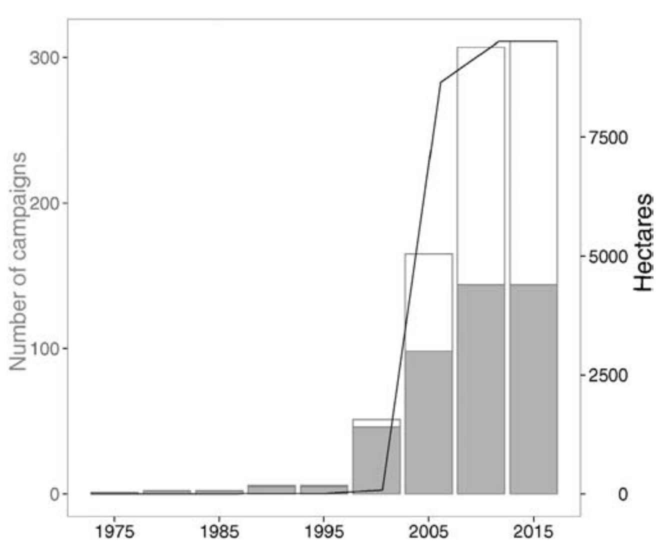

Fig. 2. Cumulative number of invasive ant eradication campaigns since 1975. About half have been successful (gray bars). The remainder of the campaigns were failures or of unknown outcome (white bars). The total global area where invasive ants have been eradicated is approximately 9500 ha (black line). Eradication campaigns using organochlorine sprays are not included.

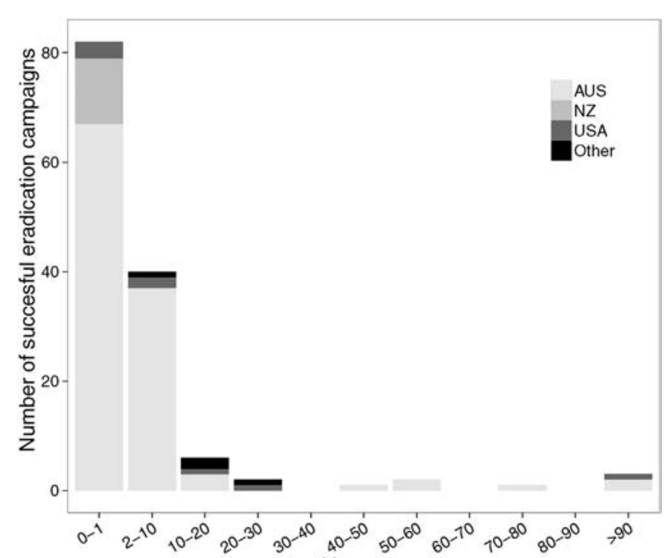

Fig. 3. Number of successful invasive ant eradication campaigns by country and size of the area targeted (when area is reported, n = 137). Most campaigns have occurred in Australia (n = 113) and have targeted areas less than 10 ha (n = 122).

originally declared free of ants. Since 2010, progress has continued with respect to eradicating invasive ants from relatively large areas. This includes the Argentine ant from three locations on Santa Cruz Island (USA, 16, 25, and 364 ha), tropical fire ant from two infestations on Melville Island (Australia, 59 and 252 ha), and *Lepisiota frauenfeldi* from Perth (Australia, 60 ha) (B. Hoffmann, unpublished data; M. Widmer, personal communication; Boser et al., 2014).

Yellow crazy ant was targeted for eradication most frequently (n = 115: 28 successes, 46 failures, 41 unknown outcome), followed by little fire ant (n = 66: 24, 0, 42) and bigheaded ant (*Pheidole megacephala*, n = 63: 49, 7, 7). However, the bigheaded ant has been successfully eradicated most often, followed by yellow crazy ant and *Solenopsis* spp. Failure rates are different among species, with campaigns targeting yellow crazy ant and Argentine ant having the highest proportion of failures (Fig. 4).

3.2. Active compounds and bait delivery

We documented sixteen AIs that have been used in ant eradications. Sixty percent (n = 174) of the campaigns that reported data used a single AI; the most commonly used were fipronil (30%) and hydramethylnon (24%), followed by a combination of fipronil and hydramethylnon (22%). Of the 192 eradications where both the outcome and AIs were documented, 90% used one or some combination of three AIs: fipronil, hydramethylnon, and a juvenile hormone mimic (Table 1). Three juvenile hormone mimics have been used successfully, usually in conjunction with other AIs: pyriproxyfen (8 campaigns), methoprene (27), and fenoxycarb (1). Other AIs used to achieve eradication, all <5 times and often in combinations, include bifenthrin, boric acid, chlordane, chlorpyrifos, diazinon, hexaflumuron, indoxacarb, orthoburic acid, sulfuramid, and thiamethoxam (Supplementary Materials).

There were differences among species for compounds and methods used relative to eradication success (Fig. 5). For example, all successful bigheaded ant eradications used hydramethylnon. In contrast, the majority of successful yellow crazy ant eradications used either fipronil alone or multiple compounds including fipronil or hydramethylnon (Table 1). Multiple compounds (commonly fipronil, hydramethylnon, and methoprene) were used in the majority of successful little fire ant and *Solenopsis* spp. eradications (Fig. 5, Table 1).

The majority of eradication campaigns used a single method to deliver bait. Fifty-seven percent broadcasted bait by hand, while 36% did so aerially by helicopter. Only 5% used multiple methods, and 2% delivered an AI by drenching nests with an aqueous solution. Nearly all yellow crazy ant eradications were conducted using aerial broadcast, while bigheaded and little fire ant eradications were conducted using hand broadcast of bait (Fig. 5). The most common bait matrix was corn (66%), either alone or mixed with protein, followed by fishmeal (21%) and paste (8%).

3.3. Non-target risks

Significant non-target impacts from the use of organochlorine sprays during ant eradications were documented prior to their banning in the 1960s and 1970s (Buhs, 2004). Those impacts are not covered here; rather, we focus on environmental risks of the most common AIs currently used (Table 2). While non-target risks are known from laboratory assessments, documentation of non-target impacts in the field is limited compared to the number of eradications, perhaps partially due to the fact that the majority of programs have occurred in small urban or industrial areas.

3.3.1. Fipronil

Fipronil is a neurological inhibitor that when ingested disrupts the nervous system by blocking receptors. It is highly toxic to fish and aquatic invertebrates, and thus its use near water should be avoided (Maul et al., 2008; Stanley, 2004). Fipronil is generally used in extremely low concentrations (e.g., 0.01–0.1 g kg^{-1}) in baits dispersed at 4–10 kg ha^{-1} (Boland et al., 2011). Although its metabolites can be more toxic than its base form, fipronil is not persistent and has low soil mobility (National Pesticide Telecommunication Network, 1997). In the only study attempting to follow its environmental fate during an ant eradication, fipronil and its metabolites were not detected in the soil one week after baiting throughout multiple baiting events over three years (Marr et al., 2003). Because fipronil is a broad-spectrum insecticide, it poses a potential threat to non-target invertebrates. It has also been shown to have impacts on vertebrates in the laboratory at low doses, particularly on bird feeding behavior, body condition, reproduction, and development (Kitulagodage et al., 2011a, 2011b). It is reported, however, as being non-toxic to waterfowl and other bird species (National Pesticide Telecommunication Network, 1997). Fipronil is moderately toxic to mammals and reptiles, but the likelihood of direct effects is low (Tingle et al., 2003).

Results from fipronil impact studies in the field are few and with mixed results. Impacts on litter invertebrates have been documented but appear limited, presumably due to the ability of invasive ants to monopolize bait (Green et al., 2004). Following a large-scale locust control program using fipronil in Madagascar, direct negative effects were documented on termites, as well as declines in lizards and tenrecs via food web effects (i.e., fipronil-induced food shortages) (Peveling et al., 2003). On Christmas Island (Australia), non-target impacts were monitored during a large-scale yellow crazy ant control program using fipronil across four treatments: aerially broadcasted, hand broadcasted, infested and not treated, and non-infested (Stork et al., 2014).

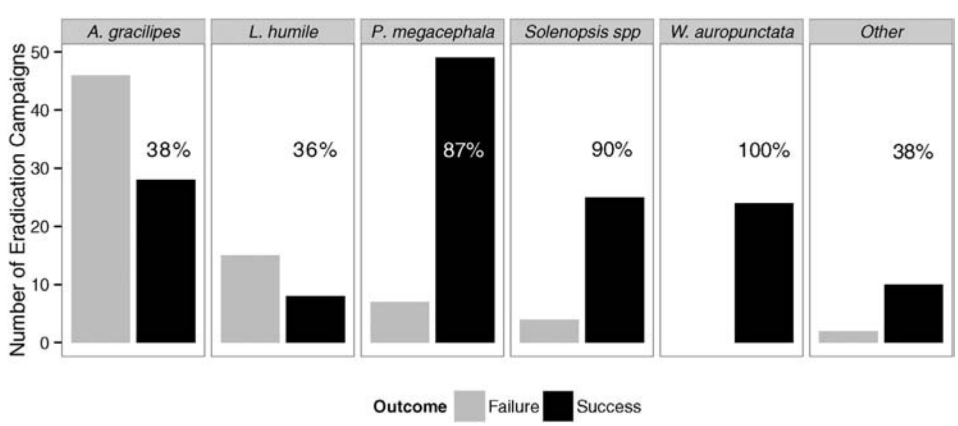

Fig. 4. Number of eradication campaigns of known outcome and overall success rate by species. Across all species, 144 campaigns have been successful and 74 have failed (66% success rate). *Solenopsis* spp. includes *S. invicta* and *S. geminata*. Other (# of programs) include *Lepisiota frauenfeldi* (4), *Monomorium indicum* (1), *Myrmecia brevinoda* (1), *Paratrechina longicornis* (4), and *Tapinoma melanocephalum* (2).

Table 1
The three most active ingredients used in invasive ant eradications: hydramethylnon, fipronil, and juvenile hormone mimics (jhm). The success rate (total number of campaigns with known outcome) is shown for each species and pooled across all species. *Anoplolepis gracilipes* (Ag), *Lepisiota frauenfeldi* (Lf), *Linepithema humile* (Lh), *Pheidole megacephala* (Pm), *Solenopsis invicta* and *Solenopsis geminata* (Ssp), and *Wasmannia auropunctata* (Wa).

Active ingredient	Ag	Lf	Lh	Pm	Ssp	Wa	All species
Hydramethylnon, jhm					100% (1)	100% (21)	100% (22)
Fipronil, jhm	100% (4)						100% (4)
Hydramethylnon			100% (1)	89% (55)	67% (3)	100% (2)	89% (61)
Fipronil, hydramethylnon	80% (10)						80% (10)
Fipronil, hydramethylnon, jhm	50% (2)				67% (3)		60% (5)
Fipronil	27% (44)	33% (3)	17% (12)				25% (59)
jhm	12% (9)			0% (1)	100% (1)		18% (11)

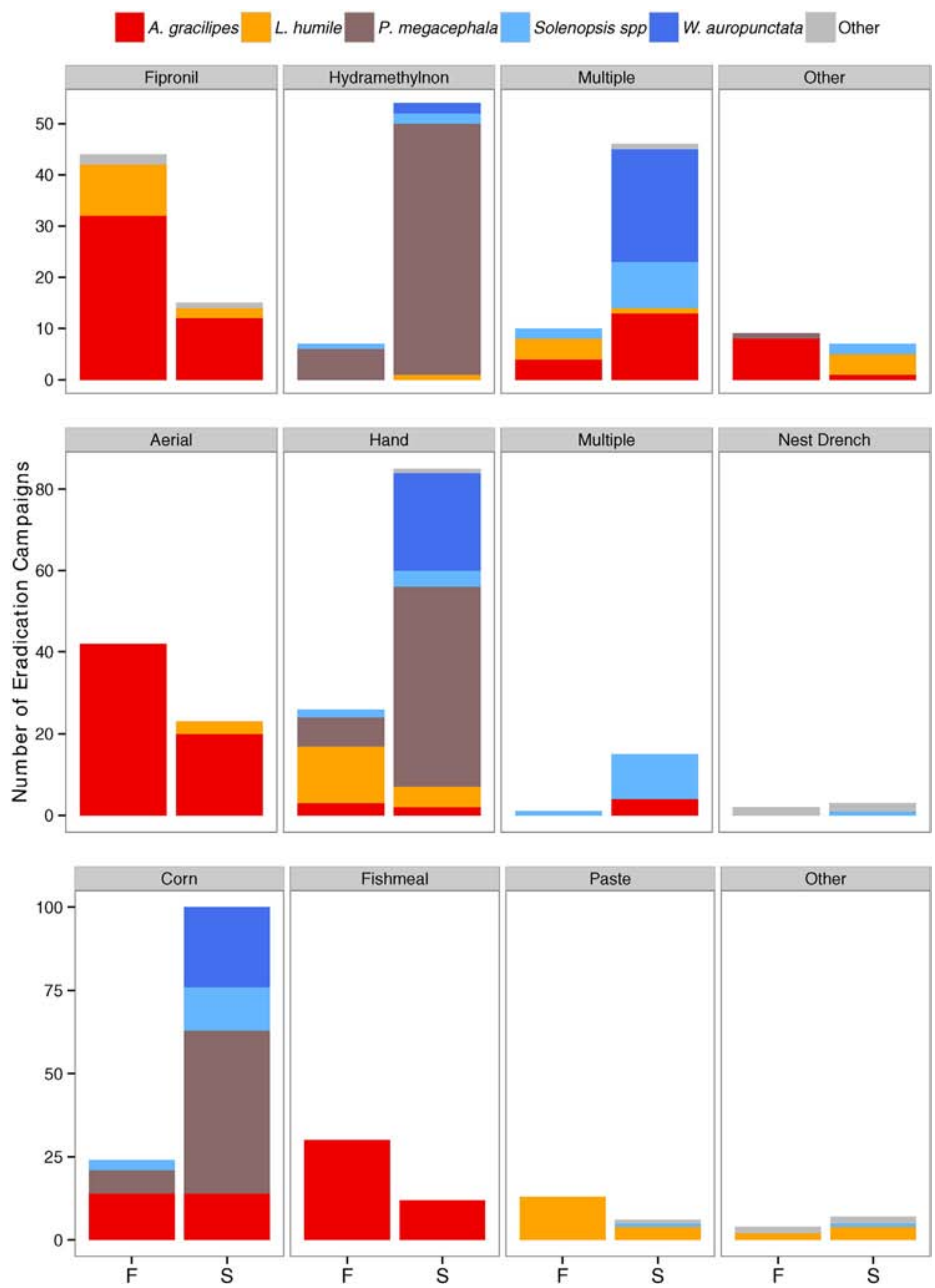

Fig. 5. Number of ant eradication programs of known outcome by active compound, bait, and method by species. Successes (S) and failures (F) are shown. Active ingredient, bait, and method are highly unbalanced with respect to species. Fipronil and hydramethylnon (and a combination of the two) are the most common compounds used. Corn and hand broadcasting are the most common bait and method used to deliver active ingredients.

Table 2
Non-target risks and description of active ingredients commonly used in invasive ant eradication campaigns.

Active ingredient	Description	Non-target risks	References
Fipronil	Slow acting broad-spectrum insecticide. Disrupts normal nerve function. Kills by contact or ingestion.	Toxic to fish, aquatic invertebrates, bees, and some birds. Toxic to small mammals if ingested. Non-toxic to earthworms and soil microorganisms.	EPA (1996), Hamon et al. (1996)
Hydramethylnon	Slow-acting insecticide that must be ingested to be effective. It kills by disrupting energy production in the cells of insects.	Toxic to fish and aquatic invertebrates, but exposure is unlikely due to it being water insoluble. Non-toxic (or low toxicity) to bees, small mammals, and most birds.	Bacey (2000), Tomlin (2000)
Pyriproxyfen	A juvenile hormone analog that prevents maturation and reproduction.	Sensitive to some aquatic insect larvae and crustaceans. Toxic to some terrestrial invertebrates. Non-toxic to bees.	De Wael et al. (1995), Ishaaya and Horowitz (1992)
Methoprene	A juvenile hormone analog that prevents maturation and reproduction.	Toxic to some fish and aquatic invertebrates. Slightly toxic to some birds. Non-toxic to earthworms and bees.	EPA (2001), Kidd and James (1991), Zoecon Corporation (1974)

No significant differences were detected in the abundance of diversity of arthropods across the four treatments. Four bird species and one reptile were monitored. The abundance of the Christmas Island white-eye (*Zosterops natalis*) was lower in non-treated control areas than in non-infested or aerially broadcasted sites. Eight months after baiting, the abundance of the Christmas Island Imperial Pigeon (*Ducula whartoni*) was lower in aerially-baited sites than in non-infested sites, and the overall abundance had significantly declined across all treatments (Stork et al., 2014).

Both red (*Gecarcoidea natalis*) and robber (*Birgus latro*) crabs are susceptible to fipronil. On Christmas Island, the non-target impacts on the former have been minimized because a) they are in low abundance due to impacts by ants, b) they do not appear to be attracted to bait, and c) control programs are conducted during the dry season when red crabs are in burrows (Green et al., 2004). Non-target impacts on robber crabs, which are attracted to bait, have been minimized with the use of bait lures located just outside of treatment areas (Boland et al., 2011). Bait-related mortality of robber crabs in treatment areas was reduced from 15% to 5% with the use of bait lures (Boland et al., 2011; Green et al., 2004).

3.3.2. Hydramethylnon

Hydramethylnon is a metabolic inhibitor that when ingested blocks the formation of adenosine triphosphate (Hollingshaus, 1987). Compared to fipronil, hydramethylnon poses a lower risk to non-target invertebrates because it is not absorbed through the cuticle. However, there is some risk to scavenging arthropods consuming bait (Stanley, 2004). With the exception of fish, it is generally of low toxicity to vertebrates (Hartley and Kidd, 1991). Hydramethylnon degrades rapidly in sunlight, and it is thought to have low persistence in the environment (Vander Meer et al., 1982).

A few eradication and control programs using hydramethylnon have investigated non-target impacts. During a bigheaded ant eradication on Lord Howe Island (Australia), no evidence of native ant or other arthropod impacts were detected in treated areas compared to control sites (Hoffmann, 2014a). On Cousine Island (Seychelles), a control program using bait stations effectively suppressed bigheaded ants with no detectable negative impacts on non-target arthropods; rather, soil surface arthropods increased following control efforts (Gaigher et al., 2012). On Midway Atoll (Hawaii), an eradication targeting tropical fire ant had a negative impact on other ant species, cockroaches (Order: Blattaria), and crickets (Orthoptera: Gryllidae) (Plentovich et al., 2010). The same negative effect on cockroaches was observed during another ant eradication in Hawaii (Plentovich et al., 2011). Other non-target arthropod effects were not detected; however, few native arthropods were present in the treatment areas.

3.3.3. Insect growth regulators

Insect growth regulators disrupt the insect endocrine systems affecting development, reproduction, and metamorphosis (Meir Paul, 2007). Compared to fipronil and hydramethylnon, they are slower acting: colony death can take up to 6–8 weeks (Lee et al., 2003; Stanley, 2004). Both pyriproxyfen and methoprene are juvenile hormone mimics that inhibit larvae from molting into adult stages or becoming reproductively mature. They cause a range of effects on ants that can result in the collapse of social organization and colony death (Banks et al., 1983). In laboratory and field trials, methoprene was less effective than pyriproxyfen at reducing colony size (Vail and Williams, 1995). Available data suggest juvenile hormone mimics pose a low risk to mammals or birds, but are toxic to some frogs, fish, and aquatic invertebrates (Ouellet et al., 1997; Sullivan, 2000). While juvenile hormone mimics are not specific to particular insect groups, increased specificity can be achieved through the use of specific baits. We are aware of a single ant-focused field trial that assessed non-target impacts of juvenile hormone mimics; two non-target species were locally extirpated from a site that received five treatments over two years (Webb and Hoffmann, 2013). The negative impacts, however, were short-term: the ant communities at the six treated sites were indistinguishable from controls within two years (Webb and Hoffmann, 2013).

3.4. Factors leading to successful eradication

Of the campaigns where success or failure has been determined ($n = 218$), the global success rate was 66%. In order to explore which factors predicted the success of ant eradications, we built a global model with a binary response variable (success or failure) and five potential explanatory factors: AI (i.e., fipronil, hydramethylnon, other, and multiple), eradication method (i.e., aerial, hand, multiple), location (i.e., island or continental), number of treatments (i.e., number of times an AI was applied), and treated area (number of ha). For sites with repeated eradication campaigns ($n = 30$ sites where there were between 2 and 4 separate eradication campaigns due to failures), we included only the first eradication campaign in order to avoid issues with pseudo replication ($n = 152$). We did not include interactions since the data were highly unbalanced.

We used an information-theoretical-based approach of Akaike Information Criteria (AIC) multi-model inference to compare all possible models (Burnham and Anderson, 2013). Models were ranked according to their AICc (a corrected measure of AIC for small samples), and ΔAICc was computed for each model (AICc of the model minus the AICc of the "best model"). From the ΔAICc, we computed the Akaike weights (ω). The Akaike weight can be interpreted as the estimated probability that each model in the set is the "best model"

(Burnham et al., 2011). We also calculated the importance weight of each explanatory variable by calculating the sum of the Akaike weights of the models that contained a particular variable. We calculated parameter estimates and 95% confidence intervals (CI), using model averaging with all models with ΔAICc < 7 (Burnham et al., 2011). Parameter estimates have a significant effect when the 95% CIs do not include zero. Goodness of fit test was performed using the *rms* package, and model selection was performed using the *MuMIn* package (Barton, 2015; Harrell, 2015).

The global model fitted the data well (*Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares* test; $p = 0.773$). Our analysis yielded eight models with ΔAICc < 7 (Table 3). The "best model" included AI, number of treatments, area, and method. With an importance weight of 1, there was strong support for an AI and number of treatments effect compared to other factors in the model (Table 3). The probability of eradication success using hydramethylnon was higher than the probability of success using fipronil (Table S1). Number of treatments was also significant in the model and positively correlated with eradication success (Table S1). Eradication method was also significant, with the probability of success being higher with mixed methods compared to aerial broadcast. While included in the model fitting exercises, location and area were not significant (Table S1).

Although there are observable differences in eradication success rates (Figs. 4, 5), uncovering potential mechanisms is challenging due to the unbalanced nature of eradication campaigns with respect to species, methods, and AIs, as well as potential complex interactions. Further, we were unable to include a species-level effect or interactions in our model. In sum, due to the different eradication approaches for each species, we were unable to tease apart the relative effects of species, AI, and method on eradication success. Our analysis does suggest that multiple treatments and using mixed methods can increase the probability of success, both of which are best practices for eradication campaigns targeting other invasive species (Broome et al., 2014; Cruz et al., 2009). While it appears that hydramethylnon performs better in eradications compared to fipronil, this conclusion is tentative at best without more targeted research.

Two issues limit conclusions regarding the performance of AIs: the large number of successful bigheaded ant eradications with hydramethylnon and the large number of yellow crazy ant failures using fipronil (Fig. 5). A single treatment of hydramethylnon appears to be an effective eradication strategy for bigheaded ants relative to other species (Hoffmann and O'Connor, 2004). Why this is, and whether fipronil would be as effective on the bigheaded ant remain unanswered research questions. The large number of eradication failures targeting yellow crazy ant, predominantly using fipronil, may be biased because 85% of the failures occurred within a single large eradication program in Australia, and included many campaigns that were conducted early in the program prior to the development of improved eradication methodologies (Supplementary Materials). However, the success of yellow crazy ant eradications appears to be increasing: nineteen recent campaigns that used multiple treatments of either fipronil or hydramethylnon appear successful but are awaiting confirmation (B. Hoffmann, unpublished data).

3.5. The cost of eradication campaigns

We collated ant eradication cost data, which was scarce and variable. For example, the little fire ant was eradicated via hand broadcasting from Marchena Island (Galapagos, 27 ha treated) for a total cost of \$16,380 per ha. Bait and active compounds made up ~5% of the costs, while salaries, logistics, and monitoring made up 75% of the total costs (Causton et al., 2005). Most reported eradication costs included only either full or partial implementation costs, making comparisons challenging (sensu Holmes et al., 2015). Reported costs for an 8 ha control program via bait stations on Cousine Island (Seychelles) only included materials and labor during the actual baiting phase: \$356 and 41 h per ha (Gaigher et al., 2012). In Australia, the average implementation costs for 24 bigheaded ant eradications was \$1553 per ha (Hoffmann and O'Connor, 2004).

We obtained economic data for implementation costs (i.e., bait and delivery) for 29 unpublished eradications (0.01–15 ha): 21 that broadcasted bait aerially by helicopter and eight that broadcasted by hand. Eradication cost information from Australia was converted to US dollars using the average exchange rate for 2014 (fxAverage = 0.902). All cost data were adjusted for inflation and are reported in US\$2015. The median cost for aerial and hand broadcasted eradications were \$2885 and \$822 per ha respectively. There was a significant relationship between cost and area, as well as differences between aerial and hand broadcasted eradications, with the latter being more cost effective (Fig. 6). However, 5 ha is the largest eradication with cost data that used hand broadcast. Thus, it is unclear, and perhaps unlikely, that hand broadcast would be more cost-effective than aerial methods for larger areas (Cruz et al., 2009).

3.6. Eradication planning

The decision to eradicate any invasive species, including ants, must undergo important decision-making and planning processes, which determine management actions. Eradication is different from a control program in that the latter manages impacts by sustained population reduction and is not concerned with removing the last individual. Eradication eliminates an entire population, and any campaign has three preconditions for success: 1) all individuals can be put at risk by the eradication technique, 2) individuals must be killed at a rate exceeding their rate of increase at all densities, and 3) immigration must be zero (Cromarty et al., 2002). These preconditions should be assessed carefully with respect to ant eradications because the biology of ant species can often make meeting them challenging. The decision to conduct an invasive ant eradication campaign should also be taken within a whole ecosystem context: what are the subsequent interactions and responses, both positive and negative, that may occur from the eradication effort (Zavaleta et al., 2001). Eradication should only be attempted

Table 3
Results of model fitting for eradication success, with maximum parsimony models ranked by model AICc. Eight nested models had a ΔAICc < 7. For each model, explanatory variables included (+), degrees of freedom (df), log likelihood (logLik), ΔAICc, and Akaike weight (ω). Also shown for each factor is its overall importance weight (*i*). A + indicates the inclusion of a categorical variable and the slope when a continuous variable is included.

	Active compound	Number of treatments	Method	Area	Location	df	logLik	AICc	ΔAICc	ω
	+	2.56	+	−0.02		8	−41.5	100.1	0	0.23
	+	2.45	+			7	−42.8	100.3	0.25	0.20
	+	2.31	+	−0.02	+	9	−40.6	100.4	0.31	0.20
	+	2.21	+		+	8	−41.9	100.8	0.73	0.16
	+	1.88			+	6	−44.7	102.0	1.92	0.09
	+	2.13				5	−46.0	102.3	2.28	0.07
	+	1.86		−0.002	+	7	−44.7	104.1	4.05	0.03
	+	2.12		−0.001		6	−46.0	104.5	4.43	0.02
i	1	1	0.8	0.5	0.5					

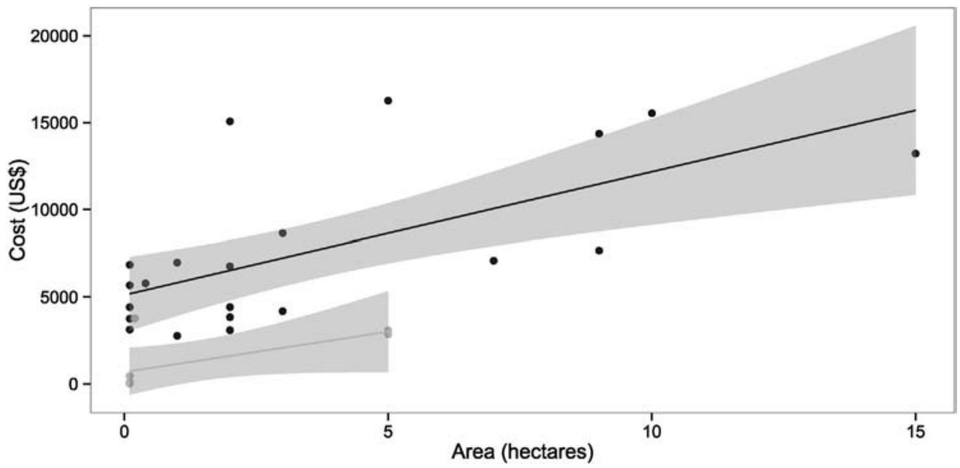

Fig. 6. Implementation costs for invasive ant eradications using hand (●) and aerial (●) broadcast. A significant relationship exists between implementation costs and area targeted ($p < 0.01$), and there are significant differences between methods (hand versus aerial broadcast, $p < 0.001$). $R_{adjusted} = 0.59$, p = <0.001, n = 29. Shaded areas are 95% confidence intervals of the fitted lines.

when the sum of benefits outweighs the costs, and success is probable within the local regulatory environment (Empson and Miskelly, 1999; Howald et al., 2010). Costs and benefits include financial, biological, and social elements, and should be evaluated on a timescale relevant to the management objectives (e.g., threatened species recovery) and consider alternatives of not undertaking eradication (i.e., the counterfactual, such as the costs of on-going impact). Similar to other invasive species, the decision to eradicate an invasive ant species will often include significant uncertainty, such as dynamics around impact and the potential for reinvasion (Hoffmann et al., 2010). Guidelines for assessing the enabling conditions for invasive species eradication and structured decision-making frameworks for environmental management are available (Empson and Miskelly, 1999; Gregory et al., 2012).

Reinvasion is a critical component to consider for any invasive species eradication campaign (Russell et al., 2008). Decision-making and planning must be done within the context of both natural (e.g., long-distance flights) and anthropogenic (i.e., human-assisted) reinvasion risk (Harris et al., 2012). Ants have limited capacity to swim significant distances but can regularly survive on flotsam and queens of some species can fly many kilometers (Heatwole and Levins, 1972). Perhaps more importantly, ants can easily stowaway on vessels, vehicles, or transported goods (Mikheyev and Mueller, 2006). Biosecurity represents quarantine and other measures established to identify and prevent reinvasion events from occurring. A biosecurity plan that identifies the necessary measures needed to prevent reinvasion should be a component of any eradication feasibility study, as well as the development of contingency procedures should reinvasion occur (Cromarty et al., 2002). The plan should reflect not only the target species' life history, but also the local conditions and potential reinvasion pathways.

Determining if and when a campaign is successful is also an important component of any invasive species eradication campaign. For many invasive species, detecting and removing the last individuals requires the most effort (Cruz et al., 2009). Confirming eradication also typically requires significant effort, and a lack of it can lead to false positives. For invasive rodent eradications in temperate latitudes, confirmation typically involves waiting two reproductive seasons (i.e., two years) whereby it would be expected that any survivors could reproduce to detectable levels (Howald et al., 2007). Recently, detection probability models have been developed for invasive rodent and predator eradication programs (Ramsey et al., 2011; Samaniego-Herrera et al., 2013). These new models provide a much-needed tool for practitioners to assess eradication success with a known confidence level and develop stop rules for monitoring.

4. Challenges and recommendations

Ant eradications are in a phase of increased research and development, with a need for increased scope and scale for application. Over the past decade, ant eradications have become more common and successful at targeting larger areas (Hoffmann et al., 2011a). Yet, the success rate (66%) is low compared to invasive mammal eradications for which data are available. For example, the success rate of mammal eradications from islands globally is 86% (DIISE, 2014). Rodent eradications are the most similar to ant eradications in the sense that current best practices include the use of a toxicant that is broadcasted over a targeted area, increasingly by helicopter because of its cost-effectiveness (Howald et al., 2007). Rodent eradications are in a more advanced phase of replication and standardized techniques. The success rate is higher (86%), while the implementation costs are lower (Howald et al., 2007; DIISE, 2014). Rodent eradications have advanced to a stage where best practices have been developed, including geographic-specific guidelines such as for the tropics which differ in important issues compared to eradications in temperate regions (Broome et al., 2014; Keitt et al., 2015). A logical next step for practitioners is to develop equivalent best practices for invasive ants, based on the best available science and eradication principles (Cromarty et al., 2002). Given the advanced stage of invasive rodent eradications and the developmental state of ant eradications, increasing communication between practitioners working in these fields should offer a valuable opportunity to improve the efficacy and cost-effectiveness of ant eradications. Below, we identify challenges to improving eradication as a tool to manage invasive ant species, as well as research priorities that can help overcome those challenges.

4.1. Natural history and taxonomic research

Our current knowledge of ant biology is limiting the ability to effectively and safely manage invasive ants, including eradication. Research is needed that seeks to integrate ant natural history with eradication strategies and methodologies. There are significant knowledge gaps around why eradications campaigns succeed or fail. We are currently limited by speculations with respect to failures, such as the possible role of certain traits like number of queens or seasonal differences in food preferences (Abbott et al., 2014; Hoffmann, 2015; Silverman and Brightwell, 2008). Similarly, we know little about the mechanisms underlying eradication success other than the treatments were likely delivered effectively to all reproductive individuals. Yet, it is increasingly clear that the natural histories of target ant species are playing a significant role in eradication outcomes (Hoffmann, 2014b; Hoffmann, 2015). Thus, more research is needed to understand how the specific traits of different invasive ant species affect eradication methodologies and efficacy. Site-specific information is likely to be most valuable (Davidson et al., 2010; Hoffmann et al., 2014). For example, site-specific information on reproductive phenology is important in determining the timing of treatments (Hoffmann, 2015). If sexual brood is present in the pupal stage during a treatment, for example, they may survive and emerge post-treatment to re-establish a colony. Research into how species' natural history affects treatment efficacy should inform the need for different eradication strategies across species. For example, it appears a single treatment of AI is capable of eradicating large populations of bigheaded ant, but numerous treatments are required for fire ants and Argentine ants (B. Hoffmann, unpublished data; Hoffmann and O'Connor, 2004). All three species typically have high-density polygynous populations, and there is no obvious aspect of their biology that would predict such different responses.

In addition to species-specific research, generalized aspects of ant natural history that may influence eradication outcomes, either positively or negatively, should also be a research priority. For example, some researchers have suggested that Allee effects could be exploited as tool to help manage invasive species, including eradication efforts for invasive insects (Suckling et al., 2012; Tobin et al., 2011). Allee effects have been documented in some invasive ant species: such effects occur in the Argentine ant and interact with queen-worker ratios in complex ways (Luque et al., 2013). More applied research on small population dynamics would likely improve practitioners' ability to manage invasive ant populations. Other targeted research could also inform ant eradications, such as resource flow within nests to queens, queen-worker dynamics, and population cycles. For example, the production of reproductive males and females is under pheromonal control of the queen, and queen removal triggers the development of brood into new reproductive individuals in some ant species (Vargo and Passera, 1991). Thus, research on methods to better target queens and how workers respond once queens are removed could improve eradication strategies and planning.

Related to ant natural history are the ecosystems and species interactions that are occurring where eradications are being targeted. For example, rodent eradications in the tropics fail at a higher rate, where non-target bait consumers often complicate eradication planning and execution (Russell and Holmes, 2015). Many ant eradications also occur in the tropics, where complex species interactions can influence impacts, strategies, and outcomes (Gaigher et al., 2013). For example, mutualistic relationship between ants and honeydew-producing hemipteran insects are common, where hemipterans (scale insects) provide ants with food in return for tending services and protection from natural enemies (Delabie, 2001). This mutualism can include non-native species from both taxa, and research on islands suggest that these species interactions may have management implications, both for invasive ants and scale insects (Abbott and Green, 2007; Abbott et al., 2014; Gaigher et al., 2013). Research on ant-insect mutualisms and other species interactions could help inform invasive ant eradication and other management strategies.

In addition to the lack of natural history knowledge, the incomplete taxonomy of ants is a challenge for improving invasive ant management. Possibly two thirds of all ant species have not been named and described (A.N. Andersen, personal communication). Even species identifications and wider taxonomic relationships of the most common and highly invasive ant species are dynamic. Taxonomic revisions are common, including purported widespread invasive ant "species" that turned out to be species complexes made up many native species with highly restricted ranges (Bolton, 2007; Hoffmann et al., 2011b; Seifert, 2003). In contrast, due to the major morphological differences of the bigheaded ant across its global distribution, it was only recently confirmed to be a single species (Wills et al., 2014). The incomplete and complex taxonomy of ants is a challenge and impediment to invasive species management, and thus, more research should enable practitioners to improve management actions and decisions, including eradication.

4.2. Increasing the efficacy of active ingredients and baits

More research and development into compounds, baits, and bait delivery are needed. Which compounds are most effective against which invasive ant species is unclear. This is largely due to species-AI bias: that is, certain AIs tend to be used for certain species as a result of industry decisions for bait creation and AI ownership. Randomized control trials in the laboratory and field that explore the efficacy of the predominant AIs across species would contribute significantly to informing best practices. Similar approaches have been used for invasive rodent eradications (Donlan et al., 2003; Witmer et al., 2014). Due to its extended effect and reduced non-target risk, research focused on the potential of increased efficacy by combining the use of juvenile hormone mimics with faster-acting compounds could be useful. For example, there were zero failures out of 22 little fire ant eradications when hydramethylnon and methoprene were used (Table 1). This combination, however, has not been used for any other species. Related to the AI is the bait matrix used to deliver it. Similar to AIs, many different types of bait have been used in eradication campaigns across a number of species, and species-specific best practices are not available. Randomized control trials along with bait availability studies prior to and during eradication campaigns would help identify optimal bait application rates (Pott et al., 2015). Relatedly, the development of new baits could help improve the efficacy and safety of ant eradications. For example, newly developed water-storing crystals were shown to be both targeted and effective for Argentine ants in the laboratory, field trials, and a recent successful eradication campaign in the Channel Islands, California (Boser et al., 2014; Buczkowski et al., 2014).

4.3. Minimizing and mitigating non-target risk

Non-target impacts are a major limiting factor with respect to scaling the pace and geography of ant eradications. Despite the need for invasive ant management in conservation areas, including many islands, less than 1/4 ($n = 31$) of all eradications campaigns have taken place in non-urban locations. We suspect this pattern is at least partially due to the limited capacity for ant eradications to either avoid significant non-target impacts within conservation areas or insufficient evidence to demonstrate the ability to manage non-target impacts to an acceptable level. More information is needed on non-target risks in order to regularly use ant eradication as a management tool in conservation areas. Relatedly, research thoroughly documenting the biodiversity benefits of eradications is needed, which would help inform the benefit–cost decision-making around invasive ant eradications (e.g., Donlan et al., 2002).

While non-target impacts and risk are documented for some taxa, such as land crabs (Boland et al., 2011; Hodgson and Clarke, 2014), major uncertainty exists for most taxa. Only a few eradication or control campaigns have actually documented impacts (Hoffmann, 2014a; Peveling et al., 2003; Plentovich et al., 2011, 2010; Stork et al., 2014; Webb and Hoffmann, 2013). It appears that in all cases, impacts are short-term. This is likely due to how ant eradications to date have been conducted in the sense that they cover only small portions of a broad landscape as opposed to an entire area (e.g., island). Treated areas within a mosaic of untreated areas likely minimize any long-term and significant impacts on non-target populations, as well as facilitating species recovery following an eradication campaign.

Despite minimum evidence for short- or long-term impacts on non-target species, the risk of undesirable species- and ecosystem-level impacts is uncertain. In addition to laboratory testing (e.g., lethal doses, LD_{50}), more field-based research is needed focused on documenting actual non-target exposure and impacts, especially for susceptible taxa such as other ants, other land arthropods, land crustaceans, fish, and aquatic invertebrates (e.g., Eason and Spurr, 1995; Geduhn et al., 2014). In addition, eradication campaigns, themselves, are excellent opportunities to experimentally investigate potential non-target impacts (Howald et al., 2010). We recommend that campaigns quantify impacts to the extent possible, both to assess and review the specific campaign's impacts but also to improve information and best practices for future campaigns.

In general, eradication campaigns should follow an "avoid, minimize, and mitigate" hierarchy with respect to non-target impacts. For other invasive species, novel methodologies have been developed or identified to mitigate non-target impacts, such as captive holding and the delivery of protective prophylactic treatments (Campbell et al., 2015; Howald et al., 2010). To date, few avoidance, minimization and mitigation approaches have been identified, developed, or successfully implemented for invasive ant management (Gaigher et al., 2012; Stork et al., 2014). Research into developing a portfolio of methodologies to avoid, minimize, and mitigate impacts from ant eradications should be a top priority.

4.4. Tools to declare eradication success

Post-eradication monitoring for species with limited home ranges and patchy distribution, like ants, can be challenging and cost-prohibitive. Recent work on detectability modeling has enabled practitioners to quantitatively monitor and confirm eradication success in real-time (Ramsey et al., 2009; Ramsey et al., 2011). These techniques combined with new digital data collection tools are making eradication faster, cheaper, and more effective (Parkes et al., 2010; Will et al., 2015). These tools should be adopted and applied to ants, which would help overcome the challenges of monitoring and declaring eradication success. Integrating new technologies, like specialized dogs, into existing survey and monitoring methodologies could also improve the ability to monitor eradication campaigns cost-effectively (Gsell et al., 2010).

4.5. The need for alternative eradication methodologies

Complementary methods exist that can help increase the efficacy of invasive ant eradications. These include actions like habitat modifications via fire and drainage restriction (Hoffmann and O'Connor, 2004; Holway and Suarez, 2006). These modifications aim to increase stress on the invasive ant species or reduce habitat suitability. Burning temporarily reduces food sources (i.e., carbohydrates) by destroying extrafloral nectaries and killing phytophagous insects, while drainage restriction creates more open and drier environments that restrict the spread or distribution of some desiccation-sensitive species such as the Argentine ant (Holway et al., 2002; Menke and Holway, 2006). These two techniques may also promote biotic resistance from some aggressive native ant species (Hoffmann and O'Connor, 2004; Menke et al., 2007). Such modifications, however, are not always appropriate considering that some invasive ant species are associated with habitat disturbance and not all habitats are fire resilient (e.g., Colby et al., 2008). More research into complementary methods to aid current methodologies could help improve both the utility and efficiency of eradication campaigns.

Like invasive rodents, the eradication of ants currently relies completely on the use of toxicants. Along with non-target risks, the use of toxicants, even for conservation use, can spark opposition from the general public (Oppel et al., 2011). Thus, a toolkit of non-toxic and complementary methods to help manage invasive ants would likely improve the ability to eradicate. While we are unaware of any non-toxic method that has achieved eradication, it would be possible, for example, to eradicate a few newly established nests using boiling water. While the removal of nests using non-toxic methods might be an effective control method under the right circumstances (Diaz et al., 2014), it is unlikely to scale due to costs and other factors in order to be an effective eradication tool. Using natural enemies of specific ant species as biological control agents has also not achieved eradication (Callcott et al., 2011). Thus, the lack of eradications using non-toxic methods is likely due to issues with the inability to scale effectively to a landscape level. However, more research could facilitate new innovative approaches. For example, pathogenic bacteria delivered in bait may have promise as a non-toxic approach (Sebastien et al., 2012). New genomic editing approaches are garnering attention for their potential ability to manage invasive species (Esvelt et al., 2014) The development of approaches such as using Ribonucleic acid interference (RNA_i) as a species-specific toxicant would drastically improve the conservation utility of ant eradication (Campbell et al., 2015; Gould, 2007). RNA_i is already being used successfully in the laboratory for ant research, including research to understand larval development regulation in the red imported fire ant (Cheng et al., 2015).

5. Conclusions

Invasive ants continue to colonize new ecosystems and impact local biodiversity (Holway et al., 2002; Lach and Hooper-Bui, 2010). Thus, in many cases, eradication will be a desirable management action. In contrast to rodent eradications where success requires the distribution of a toxicant to every individual, only a portion of an ant population (i.e., queens) needs to be targeted for eradication. Relatedly, many invasive ant species are slow to disperse across a landscape (e.g., tens of meter year^{-1}) in the absence of human-mediated dispersal. Thus, ant eradications typically target a restricted range, not entire landscapes. While these aspects bring unique challenges, they also offer underappreciated advantages, such as minimizing non-target risks.

Invasive ant eradications have increased over the past 15 years, and more populations are being targeted for eradication. Our review documented 92 eradication campaigns currently underway. Yet, compared to other invasive species, the success rate of ant eradications is low. In order to maximize the utility of ant eradication as a conservation tool, applied research and new collaborations are needed that focus on improving the efficacy, cost-effectiveness, and environmental safety of ant eradications. Cases where the biodiversity benefits of invasive ant eradication have been explicitly documented are rare (Gaigher et al., 2012; Hoffmann, 2010). More effort to do so, along with the development of best practices, will help guide future priorities.

Given the cosmopolitan distribution of invasive ants and their documented impacts on biodiversity (Holway et al., 2002), improving the ability to safely eradicate populations would deliver significant biodiversity benefits. To date, ant eradications have been largely limited to small, urban areas. This will need to change in order to maximize ant eradication as a conservation tool. New management programs, including eradication, are particularly needed on tropical islands, where invasive ants are cosmopolitan and their distribution overlaps with many threatened and endangered taxa (Herrera and Causton, 2008; Reimer, 1994). Equally important, preventing new invasive ant introductions via biosecurity measures is paramount. Ant eradications are rapidly increasing in both size and frequency, and we envisage that ants will become a greater focus of invasive species eradication efforts globally in the coming decades.

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Appendix A. Supplementary data

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