Biol Invasions
https://doi.org/10.1007/s10530-024-03392-5

ORIGINAL PAPER

Insecticide treatment of invasive ant colonies leads to secondary ant invasions and promotes the spread of invasive ants

Grzegorz Buczkowski

Received: 19 December 2023 / Accepted: 2 July 2024

Abstract Invasive ants are among the world's most damaging invaders and are considered a significant threat to urban, natural, and agricultural habitats worldwide. Populations of invasive ants are notoriously difficult to eradicate once established and are typically managed using chemical tools, predominantly toxic baits and residual sprays. Most studies evaluating control efforts do not quantify post-treatment community-level response to control efforts, so the overall outcome of management efforts remains unknown and the efficacy of management efforts in mitigating invader impacts remains unclear. The potential of insecticide treatments to cause secondary ant invasions has not been previously examined. Secondary ant invasions, the proliferation of non-target invasive ants following efforts to suppress the dominant target invader is a potentially ubiquitous, yet rarely studied problem. Additionally, limited understanding of the interactions between co-occurring invaders can be problematic for predicting how the removal of only one invasive, a common management scenario, will affect the other invaders and native communities. The current study reports on the potential threat of secondary ant invasions following insecticide treatments and highlights future research needs to address this problem. Residual spray insecticide treatments were applied in an urban setting to control the invasive Argentine ant, *Linepithema humile*. While the study was limited to a single geographic area, results demonstrate that insecticide treatments can affect target and non-target species in unpredicted ways. Specifically, insecticides applied to control invasive *L. humile* provide effective short-term control but degrade relatively quickly and lead to secondary invasions by other invasive ants. Therefore, insecticide treatments are capable of causing secondary invasions by multiple invaders. Results demonstrate that invasive ant control is not simply precision removal of the target invader but a form of ecological disturbance with multiple positive and negative impacts on the ecosystem.

Keywords Ant control · Argentine ant · Invasive ants · Insecticide sprays · Secondary invasion

Introduction

Biological invasions are among the most challenging ecological and conservation issues facing global ecosystems today (Sala et al. 2000; Pysek et al. 2020). Human activities are a major driver of biological invasions and a recent study predicts that the number of established alien species will increase by 36% between 2005 and 2050 (Seebens et al. 2020). A wide range of human activities including global trade and travel, habitat degradation, and intentional movement

G. Buczkowski (✉)
Department of Entomology, Purdue University, 901 W. State St, West Lafayette, IN 47907, USA
e-mail: gbuczkow@purdue.edu

of plants and animals have been shown to play an important role in the spread of biological invasions (Bertelsmeier et al. 2017; Bonnamour et al. 2021). Indeed, anthropogenic activities are a major driver of biological invasions worldwide and it has been shown that countries with higher economic activity, population density, and human footprint tend to receive a greater number of invasive species (Levine and D'Antonio 2003; Taylor and Irwin 2004). Understanding the relationship between human activity and invasion is critically important given that human activity is now transforming nearly all of Earth's natural ecosystems and the number and impact of invasions are closely correlated with the intensity of human activity (Meyerson and Mooney 2007; Lin et al. 2011). Therefore, improved knowledge of drivers of human-mediated dispersal is essential for predicting future invasion risk and identifying best management options.

In terrestrial ecosystems, insects are generally the most common and damaging group of animal invaders (Bradshaw et al. 2016). Among insects, ants are a particularly prominent group of invasive species and a major threat to urban, agricultural, and natural habitats worldwide (Lowe et al. 2000; Holway et al. 2002). Globally, the frequency of invasive ants is increasing due to various factors including urbanization (Buczkowski and Richmond 2012), trade (Bertelsmeier et al. 2017), and climate change (Bertelsmeier et al. 2015a). Among invasive ants, the Argentine ant, *Linepithema humile*, is a widespread invader and a significant pest in urban, agricultural, and natural environments worldwide (Silverman and Brightwell 2008). Introduced populations of *L. humile* tend to be unicolonial, forming expansive, multi-queen and multi-nest supercolonies that dominate native ant communities (Human and Gordon 1996) and are extremely challenging to control (Silverman and Brightwell 2008; Hoffmann et al. 2011, 2016). Argentine ants are mainly associated with anthropogenic environments and are frequently a pest in urban environments (Rust and Knight 1990).

The spread and impact of invasive ants is often controlled using chemical management tools, primarily residual sprays (Rust et al. 1996), granular baits (Hoffmann et al. 2016; Shults et al. 2022), or newer approaches such as hydrogel baits (Buczkowski et al. 2014; Tay et al. 2017; Sunamura et al. 2022; Hoffmann and Quinn 2022), prey-baiting based on the use of toxicant-laden prey (Buczkowski 2016; Buczkowski et al. 2018), pheromone-assisted baiting (Sunamura et al. 2011; Welzel and Choe 2016), and horizontal insecticide transfer (Buczkowski and Wossler 2019). Despite the availability of various management tools, residual spray applications are the core of most ant control programs because they are cost-effective and can be applied quickly over large areas using spray equipment. Residual insecticide sprays are widely used to control Argentine ants, particularly in urban settings (Klotz et al. 2002; Rust et al. 2003). Spray applications typically provide fast knockdown of foraging ants, prevent them from establishing foraging trails across treated surfaces, and provide efficacy for up to 90 days post treatment depending on several factors including formulation type and the active ingredient (Rust and Knight 1990; Scharf et al. 2004). Despite the tremendous economic and ecological impact of invasive ants, effective management still faces many challenges and control failures with both liquid spray insecticides and baits are common in urban (Rust et al. 1996) and natural areas (Silverman and Brightwell 2008; Hoffmann et al. 2016). Control failures are partly exacerbated by lack of published information on the results of field efficacy studies and no insecticide has been consistently effective (Hoffmann et al. 2011). Additionally, social insects are particularly challenging to eradicate relative to non-social arthropod pests (Howse et al. 2023). The prevailing treatment strategies and product label rate recommendations are not entirely compatible with the biology of many species which often leads to control difficulties or failures (Krushelnycky et al. 2005; Silverman and Brightwell 2008; Gaigher et al. 2012; Hoffmann et al. 2016). A recent study showed that Argentine ants are able to evade areas treated with toxic baits, minimizing the entry of harmful toxicants into the nest and likely contributing to control failures (Zanola et al. 2024). There is large variation in susceptibility to insecticides across different ant species (Buczkowski 2021) and a major challenge to effective ant management is lack of comprehensive, comparative studies on the efficacy of different insecticide chemistries.

The goals for the current study were two-fold. The first goal was to perform a large-scale, season-long field experiment to evaluate the relative efficacy of various spray insecticides to control *L. humile*. Given the multitude of chemistries currently available for ant control it is important to perform comparative tests (Hoffmann et al. 2016). The a priori prediction for the study was that *L. humile* would be quickly eliminated but would gradually reclaim the treated areas via the influx of *L. humile* from nearby untreated areas as the treatments begun to deteriorate. Contrary to the prediction, *L. humile* were eliminated but replaced with several species of non-target invasive ants. A study by LeBrun et al. (2007) demonstrated competitive limitation between *L. humile* and *S. invicta* in their native range. The experimental removal of one species produced the competitive release of the other suggesting that interspecific competition is an important limiting factor for both species. Secondary ant invasions, the proliferation of non-target invasive ants following efforts to suppress the dominant target invader is a potentially ubiquitous, yet rarely studied problem. Most studies evaluating control efforts do not quantify post-treatment community-level response to control efforts, so the overall outcome of management efforts remains unknown. The second goal was to focus on the secondary invaders that emerged when the treatments started to fail between 30 and 90 DAT. The current study reports on the potential threat of secondary ant invasions following insecticide treatments and highlights future research needs to address this problem.

Materials and methods

Test site

The study was conducted on the campus of North Carolina State University, Raleigh, North Carolina (35.77°N, -78.67°W). The 540-hectare (5.4 km^2) test site, bordering Avent Ferry Road and Centennial Parkway, is comprised of numerous office and laboratory buildings interspersed with streets, parking lots, walkways, and green areas (e.g. lawns, flower beds, tree lines). Invasive ant activity at the site has been sampled regularly since 2001 and results of previous surveys show that several invasive ant species are present at the site. These include: Argentine ants (*Linepithema humile*), red imported fire ants (*Solenopsis invicta*), Asian needle ants (*Brachyponera chinensis*), and dark rover ants (*Brachymyrmex patagonicus*). Based on previous surveys (Buczkowski, unpublished data), Argentine ants and red imported fire ants have been present at the site since at least 2001, Asian needle ants first appeared around 2008, and dark rover ants were first detected in 2020. Native ants mostly include species such as little black ants (*Monomorium minimum*), thief ants (*Solenopsis molesta*), and big-headed ants (*Pheidole bicarinata*), but native species appear to have been largely outcompeted and are rarely present. Additionally, small colonies of odorous house ants (*Tapinoma sessile*) were detected in several areas throughout the study site. In urban areas, *Tapinoma sessile* is known to be highly opportunistic – it exhibits supercolony behaviors and becomes a dominant pest (Buczkowski & Bennett 2006; Buczkowski & Bennett 2008a, b). It is capable becoming established in areas previously invaded by other invasive ants, including *L. humile* (Buczkowski and Krushelnycky 2011). All plots selected for the study were areas with well documented Argentine ant presence. All Argentine ant colonies selected for the study nested in mulch beds around landscape trees (Fig. 1A). Mulched landscape trees are highly attractive to ants for several reasons. The mulch retains moisture and is a perfect microhabitat for building nests and incubating brood. The trees harbor sap-sucking hemipterans which provide honeydew for the ants. Drip irrigation around the trees provides moisture and drinking water during summer months. Additionally, the trees experience no disturbance from human activity such as mowing or foot traffic. The trees are ideal nesting and feeding sites and islands of ant activity relative to paved areas such as parking lots, streets, sidewalks which offer limited nesting and feeding resources.

Field study

Experimental replicates were individual trees with high *L. humile* activity evidenced by trails going up the trees to collect honeydew. A total of 28 trees, separated by at least 20 m buffer zones, were selected for the study, equivalent to 4 trees for each of 7 experimental treatments. To determine initial ant densities (day 0) ant activity was quantified using bait counts. To perform bait counts, a paper card baited with a blend of canned tuna and corn syrup was placed on the ground at the base of the tree and collected 1 h after placement to determine the number of ants present (Buczkowski and Krushelnycky 2011, Fig. 1B). The efficacy of 7 residual spray treatments

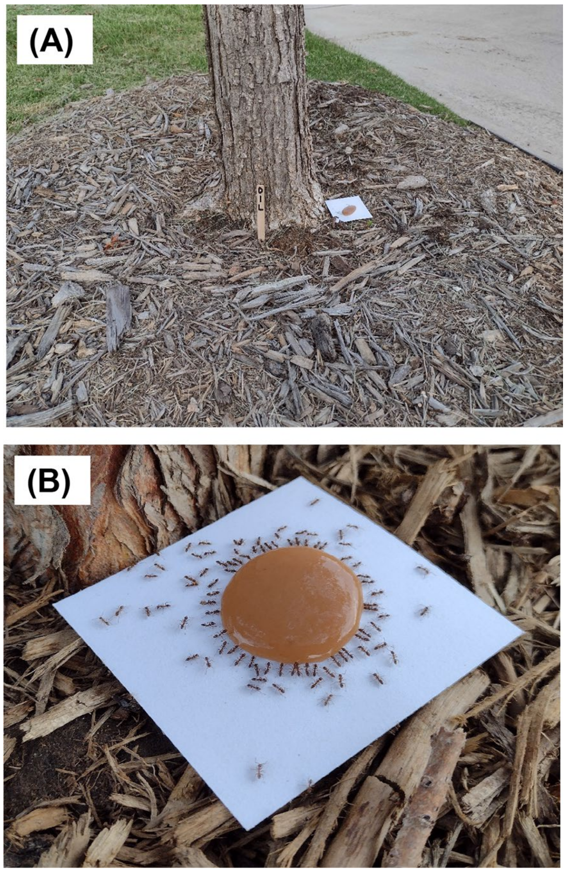

Fig. 1 **A** Urban tree islands at the study site, and **B** Argentine ants feeding on monitoring bait placed next to an experimental tree

was evaluated: (1) fipronil – low rate (0.3 g fipronil / liter), (2) fipronil – high rate (0.6 g fipronil / liter), (3) lambda-cyhalothrin – low rate (0.04 g lambda-cyhalothrin / liter), (4) lambda-cyhalothrin – high rate (0.08 g lambda-cyhalothrin / liter), (5) bifenthrin – low rate (0.4 g bifenthrin / liter), (6) bifenthrin – high rate (0.8 g bifenthrin / liter), and (7) untreated control plots. Pyrethroids (e.g. lambda-cyhalothrin, bifenthrin) and phenylpyrazoles (e.g. fipronil) are among the most common active ingredients used in residual sprays for controlling Argentine ants and other invasive ants (Rust et al. 1996; Greenberg et al. 2010; Hoffmann et al. 2016). All insecticides were commercially formulated products, but brand names are not mentioned to ensure confidentiality. The goal for the high rates was to compare the efficacy of standard rates vs. high rates (2X standard rate) to provide long-term control. All insecticides were applied at the label-recommended rate of 4 L per 100 square meters using a hand-pump sprayer. For each tree, the insecticide was applied following label directions in a 2 m radius around the tree and 0.6 m up the tree trunk, for a total of approximately 11.7 square meters of treatment area. Therefore, approximately 465 mL of product was applied for each experimental tree. The efficacy of the treatments was examined on days 1 (July 01), 3 (July 03), 30 (July 30), and 90 (September 28) using bait counts as above.

Statistical analysis

A multivariate repeated measures test was used to examine the effect of treatment, time, and the interaction on ant counts. This was followed by univariate ANOVA to examine variation at each time point. Comparisons among treatments and treatment rates-consisted of ANOVA tests on mean ant counts followed by Tukey's HSD test to test for significant differences among treatment means on each date. All statistical analyses were performed using Statistica 12.6 (Statistica 2014).

Results

The main goal of the study was to evaluate the efficacy of low and high label rates of different residual treatments to control *L. humile*—the main target invasive. In this regard, all treatments and treatment rates were highly effective and achieved 100% control of *L. humile*. Results demonstrated that all treatments and treatment rates were equally fast and resulted in complete elimination of *L. humile* from all experimental plots within 1 day (Table 1; $F = 4.31$, df = 24, $P < 0.0001$). However, it is not clear if the treatments resulted in 100% colony mortality or simply a complete elimination of workers foraging above the ground. Additionally, results demonstrated that all treatments and treatment rates were equally effective in the long-term and provided 100% control of *L. humile* for the duration of the study (90 DAT) (Table 2; $F = 13.40$, df = 24, $P < 0.0001$). The only exception was a single experimental plot treated with the low rate of fipronil where 45 Argentine ants were detected at 90 DAT (Table 1). In the case of this particular plot, it is unclear if the original colony survived the treatment and later recovered or if

Table 1 Ant counts in experimental plots treated with spray insecticides at 1, 3, 30, and 90 days after treatment (DAT)

Treatment	Replicate	initial	1 DAT	3 DAT	30 DAT	90 DAT
cyhalothrin–low rate	1	**425**	0	0	*15*	*16*
cyhalothrin–low rate	2	**350**	0	0	0	*27*
cyhalothrin–low rate	3	**400**	0	0	0	**5**
cyhalothrin–low rate	4	**525**	0	0	0	**18**
cyhalothrin–high rate	1	**245**	0	0	0	0
cyhalothrin–high rate	2	**450**	0	0	0	0
cyhalothrin–high rate	3	**200**	0	0	0	0
cyhalothrin–high rate	4	**375**	0	0	0	*45*
bifenthrin–low rate	1	**425**	0	0	0	**23**
bifenthrin–low rate	2	**475**	0	0	*25*	*34*
bifenthrin–low rate	3	**275**	0	0	0	*12*
bifenthrin–low rate	4	**250**	0	0	0	*9*
bifenthrin–high rate	1	**175**	0	0	0	0
bifenthrin–high rate	2	**275**	0	0	0	*17*
bifenthrin–high rate	3	**450**	0	0	0	*8*
bifenthrin–high rate	4	**415**	0	0	0	*11*
fipronil–low rate	1	**450**	0	0	0	0
fipronil–low rate	2	**220**	0	0	0	0
fipronil–low rate	3	**190**	0	0	0	0
fipronil–low rate	4	**475**	0	0	0	**45**
fipronil–high rate	1	**175**	0	0	0	0
fipronil–high rate	2	**420**	0	0	0	0
fipronil–high rate	3	**350**	0	0	0	0
fipronil–high rate	4	**200**	0	0	0	0
untreated control (UTC)	1	**150**	**125**	**75**	**95**	**185**
untreated control (UTC)	2	**275**	**325**	**350**	**250**	**195**
untreated control (UTC)	3	**425**	**245**	**265**	**500**	**500**
untreated control (UTC)	4	**450**	**475**	**500**	**500**	**500**
Argentine ants	*Asian needle ants*	**Red imported fire ants**	Dark rover			
ants	No					
ants						

Table 2 Mean ant counts (± st dev) in experimental plots treated with spray insecticides at 1, 3, 30, and 90 days after treatment (DAT). Means within columns followed by the same letter are not significantly different based on Tukey's HSD test (P ≤ 0.05)

Product	initial	1 DAT	3 DAT	30 DAT	90 DAT
fipronil–low rate	425 ± 74 a	0 ± 0 a	0 ± 0 a	4 ± 8 a	17 ± 9 a
fipronil–high rate	318 ± 115 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	11 ± 23 a
cyhalothrin–low rate	356 ± 111 a	0 ± 0 a	0 ± 0 a	6 ± 3 a	20 ± 11 a
cyhalothrin–high rate	329 ± 127 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	9 ± 7 a
bifenthrin–low rate	334 ± 150 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	11 ± 23 a
bifenthrin–high rate	286 ± 118 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
untreated control (UTC)	325 ± 140 a	293 ± 147 a	298 ± 177 a	336 ± 199 a	345 ± 179 a

the colony was eliminated and the area was later re-invaded by a new colony of *L. humile*. Such determinations are difficult to make and require the use of molecular markers to track colony identity throughout the study (Shults et al. 2022).

The second goal for the study was to focus on the secondary invaders that emerged when the treatments started to fail between 30–90 DAT. Results were highly dependent on individual treatments and treatment rates. Both rates of cyhalothrin were effective for up to 30 days and resulted in complete elimination of Argentine ants from all experimental sites. However, the high rate was significantly more effective relative to the low rate at 90 DAT ($F = 15.37$, df = 7, $P = 0.001$). The low rate of cyhalothrin resulted in secondary invasions at 4 out of 4 replicate sites while the high rate resulted in secondary invasions at 1 out of 4 sites (Table 1). Both rates of bifenthrin maintained high efficacy for at least 30 days, but both resulted in secondary ant invasions at 90 DAT. The high rate was not significantly more effective than the low rate ($F = 32.20$, df = 7, $P = 0.1$). Fipronil was highly effective and both rates maintained 100% efficacy for > 90 DAT. None of the sites treated with fipronil experienced secondary invasions.

Discussion

Results suggest that pyrethroid insecticides such as cyhalothrin and bifenthrin provide effective short-term control but often lead to secondary invasions. In contrast, phyenylpyrazole insecticides such as fipronil provide long-term control and typically do not result in secondary invasions. The colonization of experimental plots treated with pyrethroid insecticides by the secondary invaders suggests that the insecticides were no longer bioavailable to the incoming ants. However, the exact fate of the insecticides is unknown as they may have degraded, been washed away, or bound by the substrate (e.g. soil, mulch) and no longer effective. Previous comparative studies evaluated pyrethroid and phenylpyrazole insecticides for ant control and studies reported that all treatments led to substantial reductions in ant numbers relative to untreated controls (e.g. Soeprono and Rust 2004, Scharf et al. 2004, Jiang et al. 2014). Additionally, previously published studies reported that fipronil was the most effective treatment and provided long-term control of > 8 weeks (Scharf et al. 2004). In contrast, pyrethroid insecticides generally provided fast knockdown and satisfactory control, but treatments started to fail approximately 2–4 weeks after initial application (Soeprono and Rust 2004, Scharf et al. 2004, Jiang et al. 2014). Studies on the horizontal transfer of pyrethroid vs. phenylpyrazole insecticides demonstrated that fipronil was readily transferable among individuals resulting in high mortality rates. In contrast, bifenthrin and cyfluthrin, were less transferable. Fipronil had a significant advantage over pyrethroids because of longer delay in the onset of toxic symptoms (Soeprono and Rust 2004). Insecticides with longer residual activity and delayed action result in more ants returning to the nest and transferring the insecticide to nestmates. (Table 2)Query

The current study demonstrates that insecticide treatments are capable of causing secondary ant invasions whereby the suppression of the target invader is followed by the increase in abundance of non-target invaders. Predicting community-level consequences in multiply invaded ecosystems requires an understanding of both the interactions between co-occurring invaders and their combined impacts. In the current study, the ecological community comprised an assemblage of native and invasive ants occupying a 540-hectare urban habitat. A modeling study demonstrated that the suitable range of several highly invasive ants overlaps substantially creating high potential for invasion “hotspots” where multiple invasive species overlap and compete for resources (Bertelesmeier et al. 2015a). In invasive ants, ecological dominance is the result of several traits including high levels of aggressiveness and high interference ability (reviewed in Holway et al. 2002). Behaviorally dominant species with large colonies are thought to be better able to dominate resources and thereby suppress or exclude co-occurring species. The dominance relationships among four highly invasive ant species were investigated in colony-level laboratory trials and showed that some highly invasive and highly aggressive species such as *Pheidole megacephala* were the least dominant species and almost always suffered complete mortality (Bertelsmeier et al. 2015b). Similarly, *Linepithema humile*, lost in interactions with other invasives, similar to the results observed in the current study. Interestingly, the most dominant species, *Wasmannia auropunctata*, had the smallest body size (Bertelsmeier et al. 2015b).

The Asian needle ant, *Brachyponera chinensis*, was the most prolific invader and colonized 5 sites where *L. humile* had been eradicated. *Brachyponera chinensis* has high potential for global spread (Bertlesmeier et al. 2013) and predictive modeling demonstrates that climate change may significantly increase its global spread by increasing the amount of habitat suitable to their invasion by 65% worldwide (Bertlesmeier et al. 2013). In North America, *B. chinensis* is rapidly spreading in urban and natural areas in the southeastern United States and has emerged as an important invasive species (Rodriguez-Cabal et al. 2012; Buczkowski 2016; Eyer et al. 2018). Previous studies demonstrate that *L. humile* can be displaced by *B. chinensis*. A field study showed that *B. chinensis* are active earlier in the year when the conditions are sub-optimal for *L. humile* activity resulting in early season establishment and subsequent dominance over resources (Spicer Rice and Silverman 2013). The study demonstrated that an established invader such as *L. humile* can be displaced by a more recent invader. The displacement process observed by Spicer Rice and Silverman (2013) was based on naturally occurring interactions and was likely relatively slow. In the current study, the displacement of *L. humile* by *B. chinensis* was more indirect and was driven by human intervention consisting of insecticide application. The displacement was relatively rapid and occurred within 30–90 days post-treatment. Alternatively, it is possible that no displacement occurred and that *B. chinensis* was already present in the test plots but less affected or not affected by the treatments. Additionally, it is unclear if *B. chinensis* moved entire colonies to the newly vacated space or simply foraged there. Post-treatment surveys demonstrated that all experimental plots were free of *L. humile* within 1 day and therefore available for colonization. However, the treatments were still effective at this point and premature attempts to colonize the vacated space would have resulted in the death of the new arrivals. At untreated control sites Argentine ants persisted for the duration of the trial (and likely beyond) suggesting that Argentine ants are unlikely to be outcompeted by other invasive ants without human intervention.

The spread and impact of invasive ants is often controlled using chemical management tools and the preferred outcome of such interventions is the recovery of indigenous species following the removal of the alien invader. However, most studies evaluating control efforts do not quantify post-treatment community-level response to control efforts, so the overall outcome of management efforts often remains unknown. In the current study, native ants including little black ants (*Monomorium minimum*), thief ants (*Solenopsis molesta*), big-headed ants (*Pheidole bicarinata*), and odorous house ants (*Tapinoma sessile*) were present in several locations throughout the study site but were relatively rare and appeared to have been largely outcompeted by the invasives. Interestingly, none of the experimental plots became colonized by native ants, and all were colonized by other invasives. This suggests that in invaded urban ecosystems there is strong selection favoring invasive species that become dominant behaviorally and numerically over native species. It is plausible that the dynamics may be different in natural ecosystems which may harbor higher native diversity and abundance allowing for native species recovery. For example, ecological restoration was documented on an island in the Seychelles following a baiting treatment with hydramethylnon to control the invasive big-headed ant, *Pheidole megacephala* (Gaigher et al. 2012). The study documented "precision baiting" whereby the target invader (*P. megacephala*) experienced a rapid decline and species richness of nontarget ants and abundance of other soil-surface arthropods increased significantly after *P. megacephala* suppression. Additionally, ecological restoration was documented in a natural habitat in Australia, a rain forest site where the African big-headed ant (*Pheidole megacaphala*) was successfully eradicated using hydramethylnon bait and native ants successfully recovered approximately 2 years after the treatment (Hoffmann 2010). However, successful ant eradications are relatively rare and successful ecological restorations following successful eradications even rarer. In fact, the study by Hoffmann (2010) is the only documented case of successful eradication and subsequent recovery of the affected ecological system. It is possible that seeding areas where invasive species had been eliminated with colony transplants of native species might aid in the successful recovery of native species. However, the feasibility of such an approach has not been previously investigated and the potential benefit–cost ratio of such restoration attempts is unclear.

An obvious prerequisite for secondary invasions is the presence of other exotics to exploit the space vacated by the target invader. Pre-treatment surveys did not detect the presence of invasive ants other than *L. humile* because the study plots were purposely selected to contain only *L. humile*—the target species for evaluating efficacy of residual insecticides. However, it is possible that other ant species were present but not detected at the monitoring stations. Pre-treatment surveys using food baits would have likely detected only Argentine ants as other species would have been outcompeted by Argentine ants (Buczkowski and Bennett 2008a, b). Visual surveys of the test sites did not indicate the presence of secondary invaders prior to treatments, but it is likely that secondary invaders were present in the experimental plots or areas surrounding the plots. Similar results were observed by Plentovich et al. (2011) in a study involving the use of hydramethylnon baits to control invasive *Pheidole megacephala* ants in the Hawaiian Archipelago. The eradication of *Pheidole megacephala* was followed by dynamic compositional changes in the ant community including colonization by three species previously undetected on the island (*Solenopsis geminata*, *Tetramorium bicarinatum*, and *Anoplolepis gracilipes*). One of the new invasives, *A. gracilipes*, underwent a rapid expansion which later corresponded with reduced seabird nesting success. Additionally, similar processes have been observed in studies involving exotic plants, where secondary invasions are a rapidly emerging global problem. A study on nonnative plant removal examined how native communities assemble after the removal of multiple invasive species (Torres et al. 2023). Two highly invasive shrubs were removed at two different times in the growing season and changes in the abundances of the rest of the species in the community were monitored. Depending on the identity of the removed species, the removal of the invasive species affected community assembly by promoting other nonnative species or hindering the performance of native species. Future studies should focus on the side effects of insecticide treatments and determining how management tools may shift the balance among exotics.

The current study was conducted in an urban habitat and urban ecosystems are hotspots for biological invasions. Urban ecosystems are key points of entry for many non-native species and foci for secondary transfer into surrounding landscapes (e.g. von Heezik et al. 2010). Yet, the dynamics of biological invasions in urban habitats are poorly understood relative to biological invasions in natural habitats (Gaertner et al. 2017). The patterns and processes of urban invasions differ in many ways from invasions in other contexts, managing invasive species in cities poses unique and complex challenges, and it is unclear if fundamental concepts in the field of invasion biology are applicable to urban ecosystems (Gaertner et al. 2017). With regard to invasive ants, insecticides are frequently used to control invasive ants in urban and natural ecosystems. Yet the goals for such treatments are vastly different in these ecosystems. In natural habitats, the primary goal is to eradicate invasive species and restore native species. In urban ecosystems, insecticides are used primarily to keep populations of invasive species below a certain threshold, especially species that have high potential to be a nuisance indoors or species that are of structural and/or medical importance. Results of the current study demonstrate that insecticide treatments in urban situations may successfully reduce the abundance of an invasive pest but do not always directly translate to ecosystem recovery and may lead to secondary invasions. Similar results were observed by Scharf et al. (2004) who evaluated the effectiveness of residual insecticides in urban sites dominated by the invasive pavement ant (*Tetramorium caespitum*). The treatments led to substantial reductions in *T. caespitum* and post-treatment surveys detected the presence of odorous house ants, (*Tapinoma sessile*), a native species and a known urban pest (Buczkowski and Krushelnycky 2011; Salyer et al. 2014; Blumenfeld et al. 2021). *T. sessile* was not found in study plots before the treatments. However, a comparison of ant species composition between treated and control plots 8 weeks after the treatment revealed an increase in frequencies of *T. sessile* in treated plots only. This result highlights the invasive-like characteristics of *T. sessile* and its ability to rapidly colonize areas with vacant resources.

Results of the current study also raise important questions about ecosystem effects and the potential benefits and drawbacks of secondary ant invasions. Are the combined ecological impacts of multiple ant invaders additive or perhaps even synergistic (e.g. Jackson 2015)? Are areas invaded by a mosaic of multiple invaders “better off” ecologically than areas dominated by a single invader? Generally speaking, greater species diversity (alpha diversity) leads to greater ecosystem stability and ecosystems with higher species diversity tend to be more resilient and productive (Ives and Carpenter 2007). It might be expected that the presence of multiple invaders will lead to increased competition among the invaders and complex interactions among multiple invaders will have different fitness implications for each invader. Such interactions may in turn determine the future progression of their invasions and result in differential impacts on native species. Alternatively, the presence of multiple invaders may lead to facilitative interactions among invaders and ultimately lead to an "invasional meltdown" where the presence of many invasive species improves conditions for other invasives. Secondary invasions by multiple invaders also raise questions concerning their management. Are mosaics of multiple ant invaders easier or more difficult to manage? What are the optimal tools for managing multiple invaders that may have vastly different ecological and life-history traits? Paradoxically, the more successful the suppression of the target invader, the greater the chance that undesirable secondary invaders will become established. Future research must go beyond quantifying the target invader's response to also evaluate how natives and secondary invaders respond to management actions. Furthermore, research is needed to elucidate mechanisms favoring exotics over natives following management actions. If insecticide treatments are a significant factor driving the release of secondary invaders then the use of insecticides for conservation efforts may need to be re-evaluated (Hobbs 2007). There are important knowledge gaps to determine the effects of multiple co-existing invaders on native and urban ecosystems and such knowledge could be precious for management.

As the frequency of non-indigenous species introductions increases and their range expands, more and more ecosystems suffer invasions by multiple species. As predicted by modeling studies, vast areas around the globe will suffer from multiple invasions and it is crucial to improve our understanding of interactions among multiple invaders to better manage the invasions. This study represents a demonstration of how insecticide applications can lead to secondary ant invasions and reinforces the need for studies that include a longer temporal component to understand this process further. In particular, future studies on control efforts in conservation areas should pay close attention to the possibility of secondary invasions as well as simple re-invasion by the target species in areas where 100% control has been achieved. The insights gained from this study may provide important general lessons for invasive ant management. Insecticides applied to the environment for the control of a target species can indirectly affect non-target species in ways that are often contrary to their intended use. Future studies should aim to understand the consequences of removing only one invader in a scenario with multiple invasive species. More studies and experiments are needed on integrated management of invasive species, considering trophic interactions among invaders, hierarchies of co-occurring invasives, and interactions with native species.

Acknowledgements I thank D. Richmond for advice on data analysis and B. Hoffmann for improvements on a previous version of this manuscript.

Funding Financial support was provided in part by the Industrial Affiliates Program at Purdue University.

Data availability All data generated during the current study is provided in Table 1.

Declarations

Conflict of interest The author has no relevant financial or non-financial interests to declare.

References

Bertelsmeier C, Guenard B, Courchamp F (2013) Climate change may boost the invasion of the Asian needle ant. PLoS ONE 8(10):e75438. https://doi.org/10.1371/journal.pone.0075438

Bertelsmeier C, Luque G, Hoffmann B, Courchamp F (2015a) Worldwide ant invasions under climate change. Biodivers Conserv 24:117–128

Bertelsmeier C, Ollier S, Avril A, Blight O, Jourdan H, Courchamp F (2015b) Colony-colony interactions between highly invasive ants. Basic Appl Ecol 17:106–114

Bertelsmeier C, Avril A, Ollier S, Confais A, Diez L, Jourdan H, Orivel J, Germs NS, Courchamp F (2015c) Different behavioural strategies among seven highly invasive ant species. Biol Inv 17:2491–2503

Bertelsmeier C, Ollier S, Liebhold A, Keller L (2017) Recent human history governs global ant invasion dynamics. Nat Ecol Evol. https://doi.org/10.1038/s41559-017-0184

Blumenfeld AJ, Eyer P-A, Helms AM, Buczkowski G, Vargo EL (2021) Consistent signatures of urban adaptation in a native, urban invader ant *Tapinoma sessile*. Mol Ecol 31:4832–4850

Bonnamour A, Gippet JMW, Bertelesmeier C (2021) Insect and plant invasions follow two waves of globalisation. Ecol Lett 24:2418–2426

Bradshaw CJA, Leroy B, Bellard C et al (2016) Massive yet grossly underestimated global costs of invasive insects. Nat Comm 7:12986. https://doi.org/10.1038/ncomms12986

Buczkowski G (2016) The Trojan horse approach for managing invasive ants: a study with Asian needle ants, *Pachycondyla chinensis*. Biol Inv 18:507–515

Buczkowski G (2021) A comparison of insecticide susceptibility levels in 12 species of urban pest ants with special focus on the odorous house ant, *Tapinoma sessile*. Pest Manag Sci 77:2948–2954

Buczkowski G, Bennett GW (2005) Efficacy of simulated barrier treatments against laboratory colonies of pharaoh ant. J Econ Entomol 98:485–492

Buczkowski G, Bennett GW (2006) Dispersed central-place foraging in the polydomous odorous house ant, *Tapinoma sessile* as revealed by a protein marker. Ins Soc 53:282–290

Buczkowski G, Bennett G (2008a) Detrimental effects of highly efficient interference competition: invasive Argentine ants outcompete native ants at toxic baits. Environ Entomol 37:741–747

Buczkowski G, Bennett GW (2008b) Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*. Ecol Entomol 33:780–788

Buczkowski G, Krushelnycky P (2011) The odorous house ant, *Tapinoma sessile* (Hymenoptera: Formicidae), as a new temperate-origin invader. Myr News 16:61–66

Buczkowski G, Richmond D (2012) The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity. PLoS ONE 7(8):e41729. https://doi.org/10.1371/journal.pone.0041729

Buczkowski G, Wossler T (2019) Controlling invasive Argentine ants, *Linepithema humile*, in conservation areas using horizontal insecticide transfer. Sci Rep 9:19495. https://doi.org/10.1038/s41598-019-56189-1

Buczkowski G, Roper E, Chin D (2014) Polyacrylamide hydrogels: an effective tool for delivering liquid baits to pest ants. J Econ Entomol 107:748–757

Buczkowski G, Mothapo NP, Wossler TC (2018) Let them eat termites: prey-baiting provides effective control of Argentine ants, *Linepithema humile*, in a biodiversity hotspot. J Appl Entomol 142:504–512

Eyer P-A, Matsuura K, Vargo EL, Kobayashi K, Yashiro T, Suehiro W, Himuro C, Yokoi T, Guenard B, Dunn RR, Tsuji K (2018) Inbreeding tolerance as a pre-adapted trait for invasion success in the invasive ant *Brachyponera chinensis*. Mol Ecol 27:4711–4724

Gaertner M, Wilson JRU, Cadotte MW, MacIvor JS, Zenni RD, Richardson DM (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. Biol Inv 19:3461–3469

Gaigher R, Samways MJ, Jolliffe KG, Jolliffe S (2012) Precision control of an invasive ant on an ecologically sensitive tropical island: a principle with wide applicability. Ecol Appl 22:1405–1412

Greenberg L, Rust MK, Klotz JH, Haver D, Kabashima JN, Bondarenko S, Gan J (2010) Impact of ant control technologies on insecticide runoff and efficacy. Pest Manag Sci 66:980–987

Hobbs RJ (2007) Setting effective and realistic restoration goals: key direction for research. Restor Ecol 12:959–969

Hoffmann BD (2010) Ecological restoration following the local eradication of an invasive ant in northern Australia. Biol Inv 12:959–969

Hoffmann BD, Quinn G (2022) Honey bee death from aerosols inadvertently produced from propelled aerial dispersal of a solid bait. Pest Manag Sci 78:5213–5219

Hoffmann B, Gott K, Jennings C, Joe S, Krushelnycky P, Miller R, Webb G, Widmer M (2011) Improving ant eradications: details of more successes, a global synthesis, and recommendations. Aliens 31:16–23

Hoffmann BD, Luque GM, Bellard C, Holmes ND, Donlan CJ (2016) Improving invasive ant eradication as a conservation tool: A review. Biol Conserv 198:37–49

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) Causes and consequences of ant invasions. Ann Rev Ecol Evol Syst 33:181–233

Howse MWF, Haywood J, Lester PJ (2023) Sociality reduces the probability of eradication success of arthropod pests. Ins Soc 70:285–294

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105:405–412

Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. Science 317:58–62

Jackson MC (2015) Interactions among multiple invasive animals. Ecology 96:2035–2041

Klotz JH, Rust MK, Costas HS, Reierson DA, Kido K (2002) strategies for controlling Argentine ants (Hymenoptera: Formicidae) with sprays and baits. J Agric Urban Entomol 19:85–94

Krushelnycky PD, Loope LL, Reimer NJ (2005) The ecology, policy, and management of ants in Hawaii. Proc Hawaiian Entomol Soc 37:1–25

LeBrun EG, Tillberg CV, Suarez AV, Folgarait PJ, Smith CR, Holway DA (2007) An experimental study of competition between fire ants and Argentine ants in their native range. Ecology 88:63–75

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Lin W, Cheng X, Xu R (2011) Impact of different economic factors on biological invasions on the global scale. PLoS ONE 6(4):e18797

Lowe S, Browne M, Boudlejas S (2000) 100 of the world's worst invasive alien species. Alien 12:1–12

Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers Ecol Env 5:199–208

Plentovich S, Eijzenga J, Eijzenga H, Smith D (2011) Indirect effects of ant eradication efforts on offshore islets in the Hawaiian Archipelago. Biol Inv 13:545–557

Pysek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM et al (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534

Rodriguez-Cabal MA, Stuble KL, Guenard B, Dunn RR, Sanders N (2012) Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). Biol Inv 14:557–565

Rust MK, Haagsma K, Reierson D (1996) Barrier sprays to control Argentine ants (Hymenoptera: Formicidae). J Econ Entomol 89:134–137

Rust MK, Reierson D, Klotz JH (2003) Pest management of Argentine ants (Hymenoptera: Formicidae). J Econ Sci 38:159–169

Rust MK, Knight RL (1990) Controlling Argentine ants in urban situations, pp. 664–670. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno (eds.), Applied myrmecology: a world perspective. Westview, Boulder, CO.

Sala OE, Chapin FSI, Armesto JJ, Berlow E, Bloomfield J et al (2000) Global biodiversity scenarios for the year 2100. Science 97:1770–1774

Salyer A, Bennett GW, Buczkowski G (2014) Odorous house ants (*Tapinoma sessile*) as back-seat drivers of localized ant decline in urban habitats. PLoS ONE 9(12):e113878. https://doi.org/10.1371/journal.pone.0113878

Scharf ME, Ratliff CR, Bennett GW (2004) Impacts of residual insecticide barriers on perimeter-invading ants, with particular reference to the odorous house ant, *Tapinoma sessile*. J Econ Entomol 97:601–605

Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W et al (2020) Projecting the continental accumulation of alien species through to 2050. Global Change Biol 27:970–982

Shults P, Eyer P-A, Moran M, Chura M, Ko A, Vargo EL (2022) Assessing colony elimination in multicolonial ants: Estimating field efficacy of insecticidal baits against the invasive dark rover ant (*Brachymyrmex patagonicus*). Pest Manag Sci 78:2250–2257

Silverman J, Brightwell R (2008) The Argentine ant: challenges in managing an unicolonial invasive pest. Ann Rev Entomol 53:231–252

Spicer Rice E, Silverman J (2013) Propagule pressure and climate contribute to the displacement of *Linepithema humile* by *Pachycondyla chinensis*. PLoS ONE 8(2):e56281. https://doi.org/10.1371/journal.pone.0056281

Statistica (2014) StatSoft, Inc. Tulsa, OK, Version 1

Sunamura E, Suzuki S, Nishisue K, Sakamoto H (2011) Combined use of a synthetic trail pheromone and insecticidal bait provides effective control of an invasive ant. Pest Manag Sci 67:1230–1236

Sunamura E, Terayama M, Fujimaki R, Ono T, Buczkowski G, Eguchi K (2022) Development of an effective hydrogel bait and an assessment of community-wide management targeting the invasive white-footed ant, *Technomyrmex brunneus*. Pest Manag Sci 78:4083–4091

Tay JW, Hoddle MS, Mulchandani A, Choe DH (2017) Development of an alginate hydrogel to deliver aqueous bait for pest ant management. Pest Manag Sci 73:2028–2038

Taylor BW, Irwin RE (2004) Linking economic activities to the distribution of exotic plants. Proc Natl Acad Sci USA 101:17725–17730

Torres A, Moran-Lopez T, Rodriguez-Cabal MA, Nunez MA (2023) Timing of invasive species removal influences nonnative biotic resistance and trajectories of community reassembly. J Ecol 111:2342–2356

Welzel KF, Choe DH (2016) Development of a pheromone-assisted baiting technique for Argentine ants (Hymenoptera: Formicidae). J Econ Entomol 109:1303–1309

Zanola D, Czaczkes TJ, Josens R (2024) Ants evade harmful food by active abandonment. Commun Biol 7(1):84. https://doi.org/10.1038/s42003-023-05729-7