

## ARTICLE

# Using the red-imported fire ant to study invasive species removal and reinvasion

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**Funding information**

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**Handling Editor:** Uffe Nygaard Nielsen

**Abstract**

Invasive species are a major driver of native species declines, frequently resulting in a reduction of ecosystem function. Though control of invasive species is often beneficial, it can create other ecological issues. However, studying the results can give insight into the benefits of removal and most effective management techniques. A model invasive species to test the effects of removal is the red-imported fire ant (*Solenopsis invicta*, hereafter RIFA), which predepredates and competes with native species. We hypothesized that following removal, RIFA would recolonize treated areas from untreated borders, resulting in reinvasion and higher densities due to elimination of competition from native species that would also be extirpated by treatments. To test our hypothesis, we compared RIFA relative abundance on large sites (>400 ha) treated with a granular insecticide (Extinguish Plus, Central Life Sciences, Schaumburg, IL) in southwest Georgia, USA. Extinguish Plus effectively removed RIFA, but the treated sites were reinvaded approximately 14 months after treatment with higher densities of RIFA than on untreated areas, potentially reflecting release from competition from native ants removed by treatments. Invasive species removal may elicit a rapid recolonization via a density-dependent response mechanism and potentially increase abundance of the target species. Management strategies integrating temporal and spatial replication of control measures and multiple management techniques will be most successful in controlling invasive species.

**KEYWORDS**

Extinguish Plus, invasive species, red-imported fire ant, reinvasion, *Solenopsis invicta*

**INTRODUCTION**

Eradicating invasive species often benefits native species (Lockwood et al., 2013; Simberloff, 2014), but removing an invasive species can present its own challenges when

trying to manage for a healthy ecosystem (Courchamp et al., 2017). Uncertainty surrounds the effects of removing specific invasive species, including ecological ramifications when a well-established invasive is removed. This is problematic because temporary or permanent

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eradication has the possibility of exacerbating existing negative effects (Caut et al., 2009; Ruscoe et al., 2011; Zipkin et al., 2009). Removal is further complicated when multiple invasive species are present in an ecosystem (Ballari et al., 2016; Bergstrom et al., 2009; Zavaleta et al., 2001), a situation which likely is increasing as human disturbances increase (Airoidi & Bulleri, 2011), or when an invasive species has been established for a long time (Simberloff et al., 2013). Hence, the most appropriate method for removal and the consequences of removal should be understood when managing an invasive species (Crystal-Ornelas & Lockwood, 2020).

A model species to test the effects of removal of an invasive species from an ecosystem is the red-imported fire ant (*Solenopsis invicta*, hereafter RIFA). *Solenopsis invicta* is an invasive species in the southeastern United States that thrives in recently disturbed areas, commonly appearing in areas maintained by mowing or clearing. *Solenopsis invicta* arrived near Mobile, Alabama, around 1930 (Vinson, 1997) and has rapidly expanded its range over the past century. In its original South American range, RIFA was adapted to take advantage of natural disturbances, but in places where RIFA has invaded, anthropogenic disturbances have created a gap for the species to thrive (King & Tschinkel, 2008). *Solenopsis invicta* has high reproductive output and is an effective disperser, even without being aided by humans, allowing the species to effectively invade new ecosystems (King & Tschinkel, 2008; Lach et al., 2010; Tschinkel, 2006). As a result of its success as an invader, RIFA has cost an estimated \$5 billion USD in economic impact due to livestock and crop losses and damages as well as control costs (Fantle-Lepczyk et al., 2021).

A wide variety of native species have also been found to be negatively impacted by RIFA. For instance, RIFA has been linked to decreases in native ant and invertebrate abundance and species richness in Texas and Mississippi (Epperson & Allen, 2010; Morrow et al., 2015; Porter & Savignano, 1990). Likewise, RIFA decreases songbird nest survival (Campomizzi, 2008), predeates precocial young (Haines et al., 2017) and young reptiles (Allen et al., 1994), and impacts small mammal behavior (Darracq et al., 2016; Holtcamp et al., 2010; Pedersen et al., 2003). However, other studies have shown that RIFA density neither competitively limits native ants nor changes their species richness (King & Tschinkel, 2006; Stuble et al., 2009). In addition, native ant and arthropod diversity can even be positively associated with RIFA density (Morrison & Porter, 2003).

Given the mixed results observed when removing invasive species and the potential ecological imbalance associated with their removal, research evaluating the appropriate scale of application is much needed (Lach

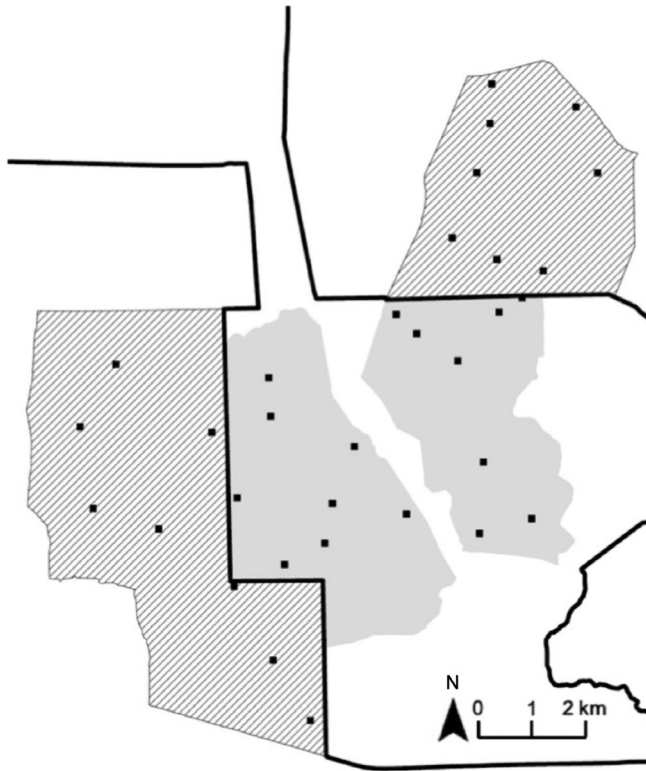
et al., 2010). Furthermore, the long-term effectiveness of removal attempts and patterns of reinvasion is poorly understood. If control is implemented inadequately, a suppressed invasive species can reinvade, and as such, reinvasion is a critical component to consider when removing an invasive species, as is evaluation of the efficacy of the treatment (Hoffmann et al., 2016). Furthermore, because chemical toxicants are recommended for controlling RIFA populations on agricultural lands (Nester, 2018), it is important to understand whether it is working as intended and what the long-term consequences are.

Using RIFA as a model invasive species, we tested the impact of removing an invasive species from large (>400 ha) treatment areas in Georgia, USA. Our study provides novel insight into the scale of application needed for temporal and spatial suppression of RIFA. Large-scale experiments are important as there can be scale-dependent responses when small plot sizes are scaled up (Carpenter, 1998; Englund & Cooper, 2003; Walters & Holling, 1990). Using a chemical toxicant, RIFA was removed to test effectiveness of removal, reinvasion patterns, and longevity of the toxicant's effectiveness. We hypothesized that after an initial decline posttreatment, RIFA would recolonize treated areas from the edges as they reinvaded from nearby, untreated areas. Because RIFA takes advantage of disturbed areas, the removal of ants with a chemical toxicant creates an easy area for RIFA to colonize (Tschinkel, 2006). We also hypothesized that following recolonization on treated areas RIFA abundances would be greater than on untreated sites. In addition to RIFA being able to quickly colonize and outcompete native ant species, the native ant species are also killed by the treatment, leaving an ecological hole for RIFA to fill. Testing these hypotheses is important for providing further knowledge about reinvasions as well as insight into the efficacy of the current methods of removal for RIFA.

## METHODS

### Study area

Our study sites comprised four large (Treated A: 505 ha, Untreated A: 870 ha, Treated B: 407 ha, and Untreated B: 472 ha) private properties located near Albany, Georgia, in Dougherty and Terrell Counties (Figure 1) managed for hunting northern bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), and white-tailed deer (*Odocoileus virginianus*). Management practices include timber volume management, prescribed fire, disking, mowing, chopping, and supplemental feeding for northern bobwhite. The sites



**FIGURE 1** Locations of ant sampling grids in a study of *Solenopsis invicta* (RIFA) reinvasion in southwest Georgia from April 2018 to September 2019. The interior of the thick black line represents the total treated area. The treated sites occur on the same property, but are separated by a buffer zone to minimize movement of individuals across replicates and maintain independence. Ant sampling grids were randomly placed across the properties (squares within experimental units)

were dominated by an overstory of loblolly pine (*Pinus taeda*) with old field ground cover and patches of longleaf pine (*Pinus palustris*). The average annual precipitation for Albany, Georgia, was 130.6 cm, with an average annual temperature of 19.0°C and summer (June, July, and August) average of 24.4°C (NOAA, 2020).

## Ant sampling

We treated experimental units ( $n = 2$ ; Figure 1) with a one-time broadcast application at 1.68 kg/ha of granular Extinguish Plus (0.365% hydramethylnon, 0.25% s-methoprene; Central Life Sciences, Schaumburg, IL) when weather conditions were appropriate (soil temperature  $>18^{\circ}\text{C}$ , low wind, and no rain forecast for 3 days). Extinguish Plus is an insecticide that kills and sterilizes ant colonies (Central Life Sciences, 2018). Decline of the colony can begin as early as a week after being treated (Central Life Sciences, 2018). Specifically, we aerially applied Extinguish Plus to the western unit in May 2018

and the eastern unit in June 2018. Application of the toxicant was applied at this time of year as it was most likely to reduce RIFA, while individuals are actively foraging and prior to peak reproduction for the colony. Untreated units ( $n = 2$ ; Figure 1), which did not receive Extinguish Plus, were chosen based on similarity in habitat and management and paired with the treated units to create replicate study areas. Treated units were separated by a distance of 450 m, meeting the assumption of independence based on mean dispersal distances of the study species. *Solenopsis invicta* queens usually fly less than 400 m before landing to create a colony (Tschinkel, 2006).

To assess changes in ant populations as well as spatio-temporal reinvasion of RIFA following treatment, we sampled ants using baited vials in  $4 \times 4$  grids with 50-m spacing that were randomly placed in both treated and untreated experimental units. We chose grid locations using stratified random sampling in ArcGIS v10.6 (ESRI, Redlands, CA). We classified the treated units into four distance bands (0–250, 251–500, 501–1000, and  $>1000$  m) from the nearest source (nontreated unit). Then, we used the Create Random Points tool within each distance band to randomly place points for grids. Two sampling grids were randomly placed in each distance band in the treated units, and an equal number of sampling units were randomly placed on untreated units, creating eight sampling grids per experimental unit.

To sample foraging ants at each point, we used a 20-ml scintillation vial baited with 1 g of hot dog (Caldwell et al., 2017; Seymour, 2007). The vial was placed on the ground, then collected 30 min later (Porter & Tschinkel, 1987), and filled with ethanol. Ants were then identified to species (MacGown, 2014) and counted in the laboratory.

We began sampling 20 min after sunrise and continued until sampling of all grids was completed, no later than sundown. All four experimental units were sampled simultaneously by separate observers. For each sampling session, observers rotated between sampling treated and untreated areas, and the order of sampling grids within each unit was systematically rotated to minimize bias from time of day and observer. Baited vials are a reliable method for sampling RIFA (Stringer et al., 2011), but not to assess relative abundance of other species of ants unless combined with additional sampling strategies (King & Porter, 2005). Therefore, only relative abundance of RIFA was assessed.

Soil temperatures of  $22\text{--}36^{\circ}\text{C}$  are optimal for RIFA foraging (Porter & Tschinkel, 1987), which was within the upper temperature range of our study area, so the heat of day was not expected to significantly reduce foraging, thereby allowing sampling to be conducted all day. However, cold temperatures are more limiting than heat, so winter temperatures would be likely to limit foraging (Tschinkel, 2006). Therefore, ant sampling consisted of one sampling session of 30 min on each grid per month

from April through September in both 2018 and 2019 to identify spatiotemporal changes. In total, we placed 6144 vials for sampling.

## Statistical analysis

We examined two indices of RIFA abundance, the proportion of vials per grid that contained RIFA and the count of RIFA for all vials in a grid for each sampling session. For each analysis, we used generalized linear mixed models (GLMM), creating a model set based on a priori hypotheses about the data. Variables considered were the following: session (all sampling that occurred for a given month), treatment (the comparison of treated and untreated properties), and distance (the distance from a sampled grid to the boundary between treated and untreated areas). Models examined comparisons of the following: a session effect, a treatment  $\times$  session interaction, and a treatment  $\times$  session  $\times$  distance interaction. Models with treatment or distance main effects without an interaction with session were considered implausible and therefore were not tested. Sampling grid was included as a random effect. Initial examinations included experimental unit as a random effect, but we omitted it because the associated random effects variance estimate was 0 for each analysis. We used nonspatial models after initial examinations of models with spatial autocorrelation in residuals indicated very weak or no autocorrelation after accounting for treatment effects.

We modeled the proportion of vials with RIFA per grid as a binomial count. Based on preliminary model fits, we determined that a beta-binomial GLMM was appropriate to account for overdispersion and clustering of vials in grid sessions (Bolker et al., 2009) with residual dispersion varying by session. We modeled the count of RIFA per grid as a negative binomial GLMM. We chose this distribution due to overdispersion in preliminary model fits resulting from a wide range of counts. For both analyses, models were fit with R package *glmmTMB* (Brooks et al., 2017; Harrison, 2015). Standard likelihood ratio tests were checked with a parametric bootstrapping comparison when the significance was between 0.001 and 0.1, using package *lme4* (Bates et al., 2015). We considered 95% CI excluding 1 on the odds ratio scale or  $p$  values  $<0.05$  as evidence of a meaningful effect. All statistical analyses were conducted in R version 3.6.3 (R Core Team, 2018).

## RESULTS

Of 6144 vials that were placed for sampling, 2849 (46.4%) contained ants when collected. Of vials containing ants,

1534 contained RIFA, 40.4% of which were on treated areas (Morehart et al., 2022). Of the 384 grids sampled over the period, only 44 (11.5%) did not contain any RIFA collections, 37 of which were on treated areas. A total of 260,651 ants were collected, of which 175,707 (67.4%) were RIFA. Untreated areas accounted for 65.0% of RIFA collections. In total, 38 ant species were identified (Appendix S1).

In beta-binomial modeling of proportions of sample vials with RIFA, the model with a session  $\times$  treatment interaction was favored over the simpler model with only a session effect ( $\chi^2 = 106.7$ ,  $df = 12$ ,  $p < 0.001$ ). There was no support for an effect of distance (likelihood ratio test of three-way session  $\times$  treatment  $\times$  distance interaction model vs. session  $\times$  treatment model) ( $\chi^2 = 40.4$ ,  $df = 24$ , bootstrap  $p = 0.054$ ). However, because our hypotheses were related to distance, we investigated the distance model to assess the biological effects of distance on treated areas over time. Overall, distance to the border did not affect the proportion of vials containing RIFA on untreated areas (95% confidence limits [CL] all bracketed 1; Table 1), but the effect of distance on the proportion of vials containing RIFA varied by session in treated areas. In several sessions, proportion of vials with RIFA increased with decreasing distance to edge, indicating higher relative abundance closer to untreated areas. For example, in July 2018, RIFA was 1.16 (1.01–1.43; 95% CL) times as likely to be present in a vial on treated areas per 100 m closer to an untreated edge. A similar effect was also observed in September 2018, and April and May 2019 (Table 1).

During July 2018 through May 2019, proportions of vials with RIFA indicated higher abundance on untreated grids than treated grids, although the exact difference was distance dependent due to the interaction. For example, in June 2018, at 500 m from the boundary edge, RIFA was 3.71 (2.12–7.18; 95% CL) times as likely to be present in a vial on an untreated grid compared to a treated grid (Figure 2). On average during this session, 48.4% (SE = 3.9%) of vials in untreated areas collected RIFA compared to only 21.9% (5.7%) in treated areas. A similar pattern was seen through May 2019. However, by August of 2019, the predicted proportion of vials containing RIFA exceeded that of untreated areas (Figure 3). In September 2019, RIFA was 1.69 (0.99–3.03; 95% CL) times as likely to be present in a vial of a treated compared to an untreated grid (Figure 2). On average in this session, 14.8% (2.0%) of vials collected contained RIFA in untreated areas, while 25.4% (2.5%) of vials collected in treated areas contained RIFA (Figure 4).

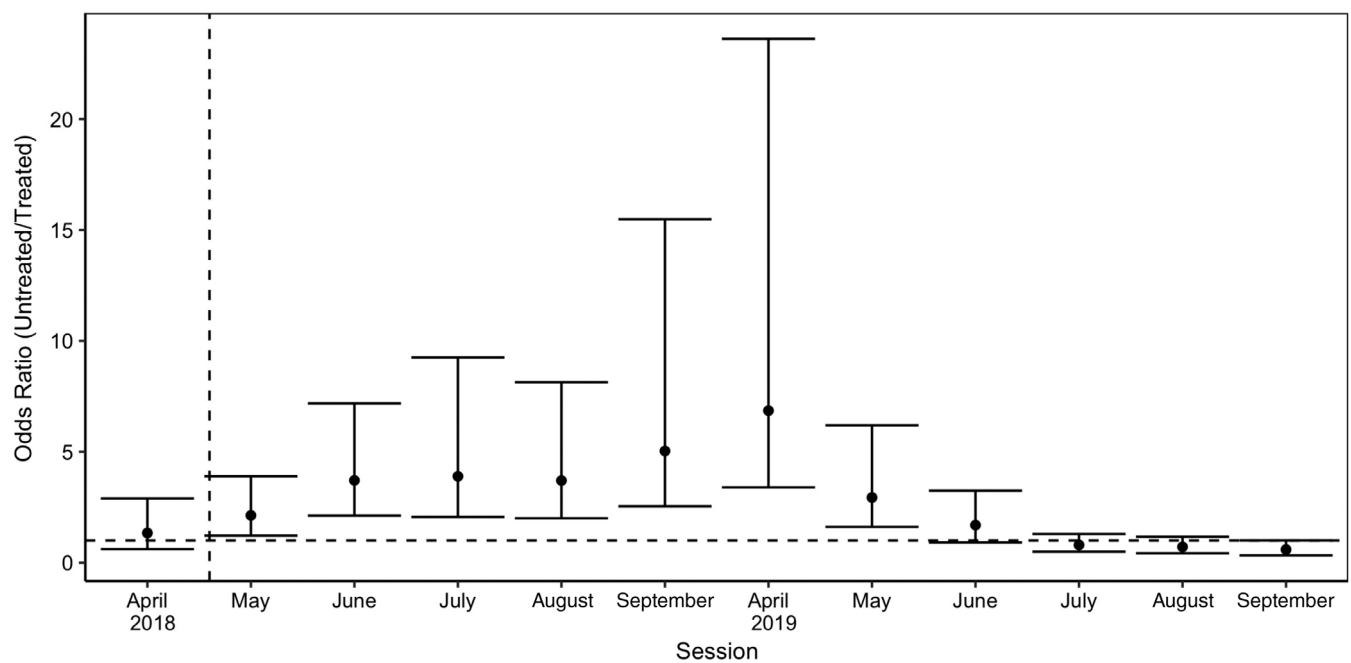
For the RIFA count analysis, the model with a session  $\times$  treatment interaction was strongly supported over the simpler model with only a session effect

**TABLE 1** Odds ratio results for the probability a vial captured *Solenopsis invicta* (RIFA) for each 100 m closer to an untreated boundary in a study on RIFA reinvasion in southwest Georgia from April 2018 to December 2019

Year	Month	Treated		Untreated	
		Odds ratio	95% CL	Odds ratio	95% CL
2018	April	0.92	(0.82, 1.02)	1.08	(0.99, 1.19)
	May	1.01	(0.92, 1.11)	1.00	(0.94, 1.06)
	June	1.10	(0.99, 1.23)	1.00	(0.94, 1.05)
	July	1.16	(1.01, 1.43) <sup>a</sup>	1.02	(0.96, 1.09)
	August	0.94	(0.83, 1.08)	0.99	(0.94, 1.05)
	September	1.16	(1.00, 1.49) <sup>a</sup>	1.01	(0.95, 1.06)
2019	April	1.16	(1.00, 1.54) <sup>a</sup>	1.00	(0.94, 1.05)
	May	1.14	(1.01, 1.33) <sup>a</sup>	0.97	(0.93, 1.03)
	June	1.00	(0.92, 1.12)	0.97	(0.92, 1.02)
	July	1.04	(0.97, 1.12)	1.04	(0.99, 1.10)
	August	0.95	(0.88, 1.01)	1.00	(0.95, 1.05)
	September	0.97	(0.90, 1.05)	1.05	(0.99, 1.12)

Note: Odds ratio of 1.0 = no effect of distance. No meaningful distance effects were detected for untreated areas, but the effect of distance on likelihood of RIFA being detected on grids varied by session for treated areas.

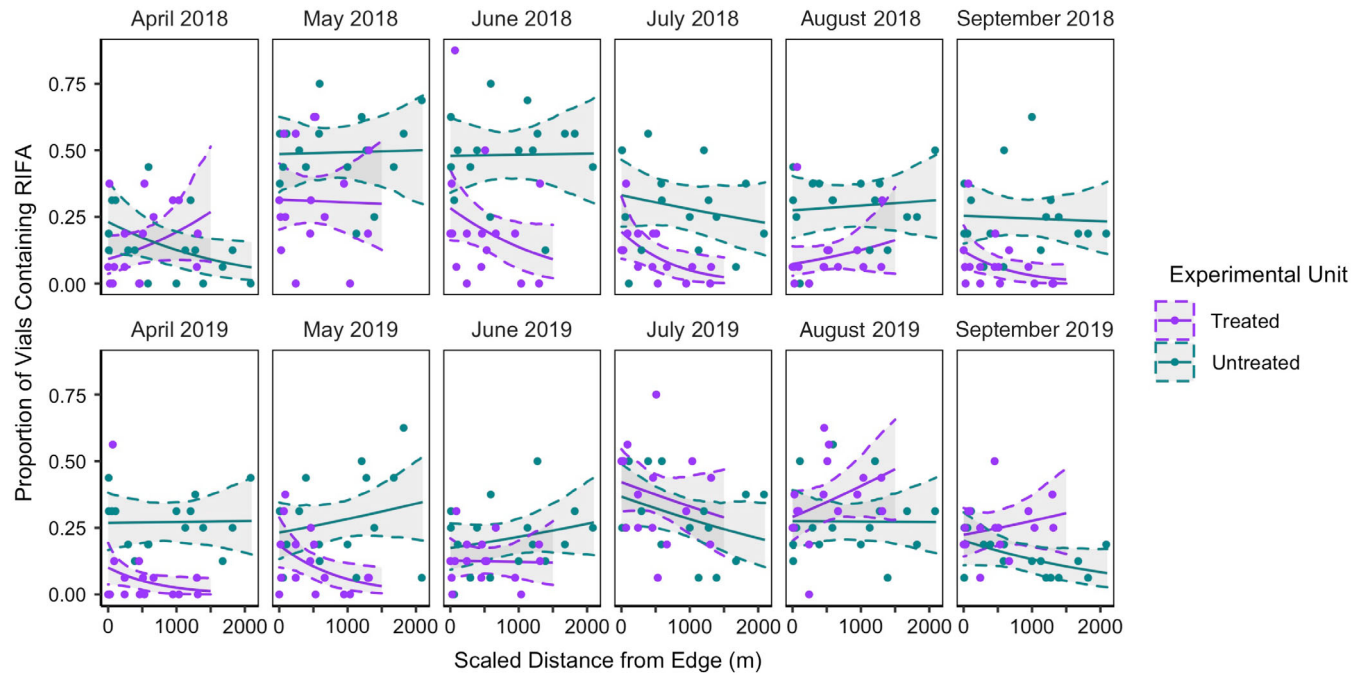
<sup>a</sup>Confidence limits (CL) do not bracket 1.



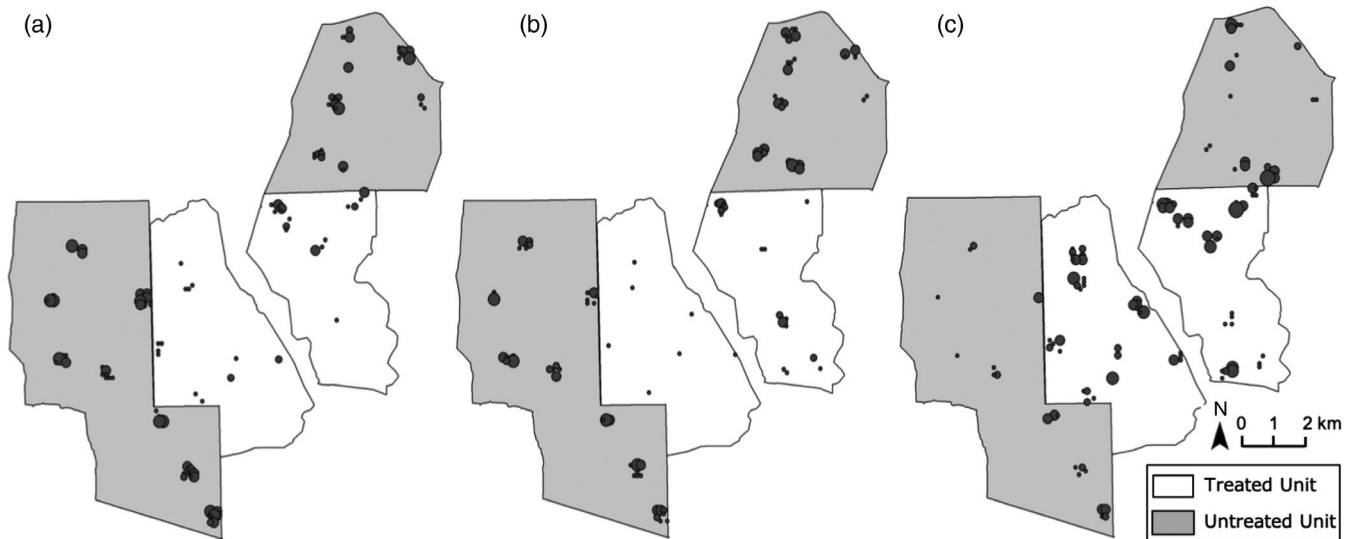
**FIGURE 2** The odds ratio (untreated/treated) of a vial containing *Solenopsis invicta* (RIFA) at 500 m from the untreated edge in a study on RIFA reinvasion in southwest Georgia from April 2018 to December 2019. A value >1 indicates higher likelihood of RIFA captures on untreated areas, while a value <1 indicates higher likelihood on treated areas, and a value of 1 (horizontal dashed line) indicates no effect. Treatments were between the April and May 2018 sampling sessions (vertical dashed line). Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect

( $\chi^2 = 71.0$ ,  $df = 12$ , bootstrap  $p < 0.0001$ ). The model with a three-way interaction of session  $\times$  treatment  $\times$  distance was not supported versus the simpler model of session  $\times$  treatment ( $\chi^2 = 33.6$ ,  $df = 24$ , bootstrap

$p = 0.22$ ). Based on the session  $\times$  treatment model, in June 2018, an untreated grid had 5.38 (1.81–16.52; 95% CL) times as many RIFA as a treated grid. Untreated grids had increasingly more RIFA than treated grids



**FIGURE 3** The session  $\times$  treatment  $\times$  distance model was not supported against the session  $\times$  treatment model, but illustrated the change in effect of distance over the reinvasion period in a study on *Solenopsis invicta* (RIFA) reinvasion in southwest Georgia from April 2018 to December 2019. Treatment was applied between the April and May 2018 sampling sessions. Dots indicate the recorded proportion of vials collected that contained RIFA. The regression line is from beta-binomial model-fitted proportions for each treatment  $\times$  session combination, with values evenly spaced across the distances with 95% confidence intervals (dashed lines)



**FIGURE 4** The number of *Solenopsis invicta* (RIFA) captured per vial varied on treated and untreated units in a study on RIFA reinvasion in southwest Georgia from April 2018 to December 2019. Dot size represents the relative number of RIFA captured in a vial. (a) In July 2018, 2–3 months posttreatment, fewer RIFA were captured on units that had been treated with Extinguish Plus. On the eastern treated unit, more RIFA were captured near the border with the untreated area than were captured in the interior. (b) In August 2018, 3–4 months posttreatment, RIFA continued to be captured in greater numbers on untreated units, but captures began to increase in some of the interior areas of the treated units. (c) By September 2019, 15–16 months posttreatment, captures of RIFA were much greater on units that had been treated than those that had not

until June 2019, when the effect neared 0 for the remainder of sampling (Figure 5).

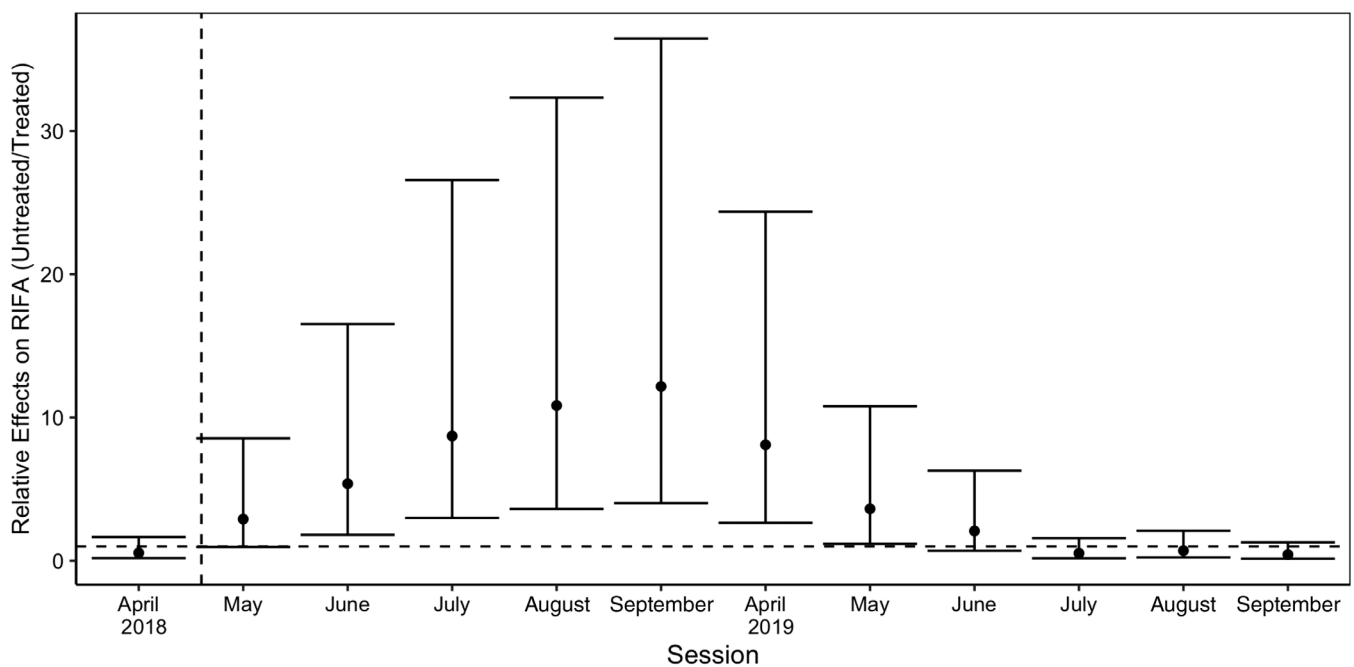
## DISCUSSION

Extinguish Plus effectively reduced RIFA abundance on treated properties, but RIFA then reinvaded and reached greater relative abundance than untreated areas by the end of the study period. Although there was evidence that proximity to the border impacted reinvasion magnitude on treated areas, the effect of distance was not important over the entire reinvasion period. These results support our hypothesis that RIFA would recolonize treated areas at higher numbers than pretreatment; however, our alternative hypothesis was not supported such that reinvasion was not distinctly and solely observed from the edges. The invasion patterns found in our study provide novel insight into the scale at which treatment is needed to adequately suppress RIFA. While Extinguish Plus effectively reduced RIFA abundance, higher RIFA numbers by the end of the study indicate potential negative ecological outcomes following treatment and underscore the need for other management techniques for invasive species control.

Distance to the edge of the treatment area was important for reinvasion in the period immediately following

treatment. Most colony founding for RIFA occurs between April and August (Tschinkel, 2006), so RIFA likely began recolonizing the treated properties immediately after treatment occurred (May–June). Because very few queens (<3%) have been reported to fly up to 400 m away to form a new colony (Tschinkel, 2006), females would begin founding new colonies close to untreated boundaries or near surviving colonies on treated areas and reinvade from there. In the months immediately following treatment (June and July 2018), RIFA was more likely to occur in the areas close to the borders and less likely in the interior of the treated property (Figure 3). Because recolonization distances are so short, the collection of RIFA from the interiors of the properties in the months following treatment indicates that some colonies did persist following treatment. As such, reinvasion likely occurred from both outside and within the treated areas.

When an invasive species is temporarily reduced, but not entirely eradicated, reinvasion is highly likely (Drees et al., 2013; Hoffmann et al., 2016; Myers et al., 2000; Zavaleta et al., 2001). In a previous study across millions of treated hectares, colonies experienced 98%–100% mortality, but reinvasion by RIFA still occurred (Williams et al., 2001). Because RIFA is an efficient invasive species and effective colonizers, they rebound quickly following disturbances and chemical toxicant treatment. Therefore, resource managers should anticipate this reinvasion



**FIGURE 5** The relative effect of treatment on *Solenopsis invicta* (RIFA) count per grid in a study on RIFA reinvasion in southwest Georgia from April 2018 to December 2019. A value >1 indicates expected captures are higher on untreated areas, while a value <1 indicates expected captures are higher on treated areas, and a value of 1 (horizontal dashed line) indicates no effect. Treatments were between the April and May 2018 sampling sessions (vertical dashed line). Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect

potential and plan repeated treatments for continued suppression of RIFA. More research is warranted to better understand how chemical toxicant can be used along border areas following initial treatment to extend its efficacy without requiring an entire additional reapplication. Similarly, evaluating how natural borders of uninhabitable or less inhabitable areas impede reinvasion for RIFA may provide more efficacious delivery of chemical treatment. For example, because RIFA thrives in disturbed areas (Tschinkel, 2006), border areas could include areas with minimal disturbance, to discourage reinvasion. Further, minimizing disturbance in treated areas may reduce temporal and spatial recolonization (Haines, 2018). We would expect that treating larger areas would result in longer recolonization times because of the increase in area further from the treatment boundary, but additional research is warranted. Our applications were conducted at larger scales of operation than other comparable studies (King & Tschinkel, 2006; Long et al., 2015; Roeder et al., 2021). Additional research at this management scale could give further insight into recolonization following toxicant use on large areas. Given our results of reinvasion, application of toxicants for RIFA should also consider the management strategies of adjacent properties to where the treatment will be applied. While there are techniques to increase the effectiveness of chemical controls (Hoffmann et al., 2010), management decisions should also consider other repercussions to the area following treatment (Simberloff, 2014).

We found that, following the single treatment of Extinguish Plus, treated areas no longer showed a difference from untreated areas in RIFA abundance 14–16 months posttreatment. Even if initially successful, removal of invasive species can have unintended consequences, resulting from density-dependent relationships and interactions within species assemblages in which populations can overcompensate for removal or take advantage of open niches of other species (Ruscoe et al., 2011; Zipkin et al., 2009). Two nonexclusive mechanisms by which RIFA could rebound to higher than original levels would be release from competition from other ants and an overcompensatory rebound driven by density-dependent mechanisms (Adams & Tschinkel, 1995, 2001; Tschinkel, 2006). Because RIFA is very territorial, reduction in intraspecific competition following treatment may allow colonies at the border to thrive and expand unimpeded by other territories. Sampling in our study targeted RIFA rather than the general ant community, but results from other studies suggest interactions with other ants limit RIFA numbers (Stimac & Alves, 1994; Tschinkel, 2006). *Solenopsis invicta* biomass across multicolony populations is regulated by density-dependent mechanisms (Adams & Tschinkel, 2001), and lagged density dependence can result in overcompensation in rate of invasive spread and abundance following partial

control (Arim et al., 2006). Regardless of whether the mechanism is due to interspecific or intraspecific dynamics, there is potential for removal efforts to increase rather than eliminate the target invasive (Moe et al., 2002; Pardini et al., 2009; Zipkin et al., 2008). Following reinvasion of RIFA in treated areas, we found that more vials containing RIFA were detected on treated areas than on the untreated areas, matching results from previous studies on RIFA density following treatment. These studies often relegate cause to elimination of native ant species that competed with RIFA (Showler & Reagan, 1987; Stimac & Alves, 1994; Summerlin et al., 1977). Alternatively, lower inter- and intraspecific competition following treatment on a highly suitable site for nuptial queens may yield a much greater number of smaller colonies posttreatment rather than similar or fewer colonies at greater abundance. Future research investigating lure colonization rates could elucidate reinvasion strategies and provide improved insight into long-term management solutions.

For RIFA and likely other invasive species, inadequate application of insecticides may only temporarily suppress populations (Drees et al., 2013). A better understanding of application scale is needed to inform control of invasives using insecticides. At small scales, long-term control of RIFA will be difficult given density-dependent responses commonly observed (Tschinkel, 2006), requiring repeated applications to extend suppression, resulting in higher management costs (Drees et al., 2013; Silverman & Brightwell, 2008). Additionally, Extinguish Plus kills native ants as well as RIFA, which in combination with the increased densities of RIFA following treatment, could lead to worse ecological impacts for native ant species than simply not treating RIFA. Removal of invasive species can lead to negative impacts on nontarget species, including reduced richness of other species (Zarnetske et al., 2010). Therefore, unless serving a specific purpose such as protecting agricultural crops, chemical treatments could be doing more damage than good (McLaughlin & Dearden, 2019). Although chemical treatment can be effective in certain situations and at large scales, other management techniques or other products such as insect growth regulators should be explored as less ecologically harmful alternatives (Rabitsch, 2011).

Given our results, alternative solutions should be explored to for effectively controlling RIFA long-term. Alternative control techniques might include biocontrol, which has proven success against agricultural pests in certain conditions (Pejchar et al., 2020). Porter et al. (1997) suggested that RIFA was more abundant in their invaded range compared with their native range due to escape from natural enemies. Valles et al. (2018) prospected viral pathogens as a self-sustaining biocontrol agent for RIFA. Even if biocontrol does not eradicate RIFA—as most



studies on biocontrol of RIFA suggest—it could reduce abundance or influence foraging enough to allow other species to better outcompete RIFA. Alternatively, biocontrol could improve suppression magnitude when coupled with chemical toxicant treatments. Integrated pest management involves using multiple tools to effectively manage a species over the long-term, a strategy which should be used for RIFA. Leaving an invasive species alone is controversial because of the unknown or future impacts they can have (Simberloff, 2014), but, in some scenarios, this might be the best strategy for long-term management of RIFA especially with long-established invasive species that may fill ecological voids in a functioning ecosystem. *Solenopsis invicta* is a long-established invasive species in the United States, and while its control or eradication may be warranted to restore the integrity of desired forest conditions, localized chemical application is ineffective and cost-prohibitive.

### ACKNOWLEDGMENTS

We thank the many field technicians who made this project possible, especially A. White, J. Rectenwald, M. Portwood, M. Cooper, and A. Jackson. We also thank two anonymous reviewers who helped improve the manuscript. This work was funded by Tall Timbers through The Robert C. Balfour Game Bird Management Fellowship, Gerry Game Bird endowment, and Pamela H. Firman Quail Management Research Initiative, and the McCrary Institute at Auburn University.

### CONFLICT OF INTEREST

The authors declare no conflict of interest.

### AUTHOR CONTRIBUTIONS

D. Clay Sisson and Theron M. Terhune II conceived the experiment. D. Clay Sisson, Morgan A. Morehart, and Theron M. Terhune II designed the experiment. Morgan A. Morehart and D. Clay Sisson carried out the field work. Morgan A. Morehart, Theron M. Terhune II, and Robert A. Gitzen analyzed the data. Morgan A. Morehart wrote the initial manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

### DATA AVAILABILITY STATEMENT

Data (Morehart et al., 2022) are available from Aurora: <https://doi.org/10.35099/aurora-93>

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Morehart, Morgan A., Robert A. Gitzen, Theron M. Terhune II, Christopher A. Lepczyk, and D. Clay Sisson. 2022. "Using the Red-Imported Fire Ant to Study Invasive Species Removal and Reinvasion." *Ecosphere* 13(7): e4075. <https://doi.org/10.1002/ecs2.4075>