

5-2018

Experimental evidence that the non-native European fire ant alters invertebrate communities

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Recommended Citation

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Experimental evidence that the non-native European fire ant alters invertebrate communities

by

Madeson C. Goodman

An Abstract of a Thesis in Biology

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Arts

May 2018

Buffalo State College
State University of New York
Department of Biology

ABSTRACT OF THESIS

Successful non-native species can reduce native species richness through both direct and indirect competition. Many invasive ants, such as the European fire ant (*Myrmica rubra*), are particularly successful invaders due to their ability to form multi-nest, multi-queen “supercolonies” that appear to displace native ant and non-ant invertebrate fauna in invaded regions. *Myrmica rubra* has invaded the Northeastern United States, including Tiff Nature Preserve in Western New York, but its seemingly negative impacts on local invertebrate communities have only been assessed using correlative studies, making it difficult to determine whether these ants directly displace native ants and invertebrates or are simply better suited for different habitat conditions than the natives. I surveyed Western New York parklands to investigate native ant and non-ant invertebrate abundance in *M. rubra*-invaded and uninvaded areas. I then tested these observations with an ant pesticide treatment targeting *M. rubra* at Tiff Nature Preserve to investigate the direct impacts of *M. rubra* on the native ant and invertebrate community and potential cascading effects on leaf decomposition. A consistent, negative relationship was found between *M. rubra* and native ants in both the observational and experimental research, and native ant species only appeared in the pesticide-treated plots with reduced *M. rubra* abundance. These data strongly suggest that *M. rubra* actively displaces the native ants with invasion. *Myrmica rubra* appeared to share habitat with non-ant invertebrates in both the observational and experimental research, and the removal of *M. rubra* resulted in increased predatory invertebrate populations and a subsequent decrease in invertebrate prey species. I found no effect of *M. rubra* reduction on leaf litter decomposition. Nevertheless, these results indicate that *M. rubra* is negatively impacting native ant communities, and even though implementing a targeted pesticide

may help native ant populations rebound, the removal of *M. rubra* may negatively impact invertebrate detritivores.

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A thesis submitted in partial
Fulfillment of the Master of Arts degree
in Biology at Buffalo State College

May 2018

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ACKNOWLEDGEMENTS

I would like to thank my committee members, Dr. Robert Warren II, Dr. Amy McMillan, Dr. Christopher Pennuto, and David Spiering, for their guidance along the way and commitment to my academic success. Thank you all for sharing your time and knowledge with me. A special thanks to my advisor, Dr. Robert Warren, for his enthusiasm, support, and willingness to work with me despite my strong sense of independence. Your passion not only for my project, but for everything you do, is inspiring, and I am so grateful for your help in achieving my goals.

Thank you to Zach Goodrich at Tiff Nature Preserve for providing access to my study site and for your help in the field. Thank you to the Buffalo State Biology Department, Dr. Martha Skerrett, and Sue Chislett for your help with anything and everything I needed during my time at Buffalo State. I'd also like to thank my fellow graduate students for all of the advice and friendship we've shared over the past two years.

To Abby Mathew – thank you for your help in the field and for your friendship. I have really enjoyed working with you for the past two years and I look forward to hearing all about the great successes the future has in store for you. To Kazz Archibald and Camille Dorset – I am very grateful for the invaluable help you provided me in both the field and the lab.

Finally, I would like to thank Brodie Fenton for helping me every step of the way. Thank you for driving all around Western New York with me to flip logs and count bugs, for keeping me grounded, and for believing in me even when I didn't believe in myself. I am so grateful every day for your unconditional love and support.

I'd like to dedicate this work to my parents, without whom none of this would have been possible. I appreciate everything you have done and continue to do for me more than I know how to express.

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Introduction

Non-native species can simplify native assemblages by outcompeting native species with similar niche requirements (Mooney and Cleland 2001, MacDougall et al. 2009) and by directly exploiting native fauna as prey (Zavaleta et al. 2001, Verble-Pearson and Pearson 2016). If successful, a non-native species can dominate a native system (Zavaleta et al. 2001, MacDougall and Turkington 2005) and may subsequently reduce native community composition, abundance, and biodiversity (Olden and Rooney 2006, Wardle and Peltzer 2017). However, the establishment and persistence of a non-native species often are influenced by the physical environment as well (Hobbs and Huenneke 1992, Holway et al. 2002). Thus, it is difficult in most cases to determine the role of a non-native species as either passive or active in their establishment and dominance (MacDougall and Turkington 2005, King and Tschinkel 2008).

Interspecific competition often structures ant communities (Hölldobler and Wilson 1990), and many non-native ant species are exceptional competitors and predators (Mooney and Cleland 2001, Gibb and Hochuli 2003). Successful non-native ants, such as *Linepithema humile* and *Solenopsis invicta*, are omnivorous, generalist predators that can exploit nest sites in various habitats and climates (Mooney and Cleland 2001, Groden et al. 2005, Bertelsmeier et al. 2016). Additionally, non-native ants are often polydomous (multi-nest) and polygynous (multi-queen), resulting in densely populated “supercolonies” that allow collective exploitation of resources and rapid expansion of genetically related populations (Elmes and Petal 1990, Porter and Sauvignano 1990, Holway et al. 2002, Garnas et al. 2007). Because native and non-native ants often share niche requirements (Parr and Gibb 2009, Warren et al. 2015), competitive exclusion may explain the oft-observed displacement of native by non-native ants (Gibb and Hochuli 2003, Groden et al. 2005, Hicks et al. 2014). For example, *Aphaenogaster rudis* (and the closely related congener

A. picea) is a dominant native ant species in temperate forests (King et al. 2013) and *Brachyponera chinensis* invades *A. rudis*-dominated forests, replacing *A. rudis* as a termite predator and displacing it from downed wood nesting sites (Warren et al. 2015). Additionally, the invasive Argentine ant (*L. humile*) uses its high population densities and direct aggression to reduce native ant foraging success in invaded regions such as California (Human and Gordon 1996, Holway 1998b, Holway et al. 2002) and displace native arboreal ants from trunk nesting sites in Spain (Carpintero et al. 2005). Studies conducted on another highly invasive ant species, *Solenopsis invicta*, also have found strong negative correlations between *S. invicta* and native ants (Porter and Sauvignano 1990, Gotelli and Arnett 2000, Cook 2003), but work by King and Tschinkel (2008) suggests that *S. invicta* actually prefers anthropogenically altered habitat avoided by native ants. In general, non-native species, including ants, often thrive with human disturbance (King and Tschinkel 2008, Stuble et al. 2009, Michlewicz and Tryjanowski 2017), though non-native and native ants often share niche requirements and are both generally well-suited for similar habitats (Parr 2008, Parr and Gibb 2009). Hence, decoupling the habitat preferences of non-native ants from their active competitive and predatory abilities is a prominent challenge in understanding the success of ant invaders.

Non-native ants can also impact invertebrate communities either through competition for shared resource requirements or directly through predation (Boser et al. 2012, Naumann and Higgins 2015, Verble-Pearson and Pearson 2016). For example, in addition to its effects on native ants, *S. invicta* also decreases both the abundance and diversity of native invertebrate communities where it occurs (Porter and Sauvignano 1990). However, Hanna et al. (2015) observed little impact of *L. humile* invasion on arboreal invertebrates, including spiders and bark lice, and Rowles and Silverman (2010) observed minimal *L. humile* foraging on branches.

Ground-dwelling invertebrates, such as ground beetles and millipedes, may therefore be the most heavily affected by ant invasions due to shared niche requirements and availability as prey for non-natives (Parr and Gibb 2009, Bertelsmeier et al. 2016, Parr et al. 2016). Many of these ground-active invertebrates, such as millipedes and isopods, are important leaf litter decomposers in temperate terrestrial ecosystems (Hassall et al. 1987, Lavelle et al. 1992, Bogyo et al. 2015), and the negative influence of non-native ants on these detritivore communities may also alter ecosystem decomposition processes (Zimmer et al. 2005, Parr et al. 2016, Wardle and Peltzer 2017).

The European fire ant, *Myrmica rubra*, is a Eurasian ant species that has invaded coastal areas of North America. In their native Eurasian range, *Myrmica* ants are keystone species, acting as hemipteran-tenders in exchange for honeydew sugars (McPhee et al. 2012, Novgordova and Gavriljuk 2012), symbiotic hosts to rare lycaenid butterflies (Thomas et al. 1989, Elmes et al. 1998), and seed dispersers for myrmecochorous plant species (Gorb and Gorb 1999, Fischer et al. 2005). *Myrmica rubra* also appears to possess many characteristics of successful invasive ants, such as omnivory (Gorb and Gorb 1999) and the ability to do well in anthropogenically altered habitat (Michlewicz and Tryjanowski 2017). In their invaded range, *M. rubra* ants are polygynous and polydomous (Elmes 1973, Groden et al. 2005, Garnas et al. 2007) and feed via trophallaxis (consumption and regurgitation) (Cassill and Tschinkel 1996, Groden et al. 2007). Non-native *M. rubra* also reproduce solely through budding, in which a queen and several workers break off from the colony and occupy a new nest space (Elmes and Petal 1990). Together, these characteristics allow the formation of an extensive supercolony network of *M. rubra* at invaded sites in their non-native range (Groden et al. 2005).

Myrmica rubra has invaded many areas in the Northeastern United States, such as Tiff Nature Preserve (Tiff) in Buffalo, New York (Spiering 2009, Warren et al. in review), likely via ship ballast and ornamental plants (Grodén et al. 2005, Hicks et al. 2014). Native ant and other invertebrate abundance and richness generally decline with *M. rubra* in N. America (Garnas et al. 2014, Naumann and Higgins 2015, Verble-Pearson and Pearson 2016). For example, Garnas (2014) observed the displacement of native ant foragers by *M. rubra*, and Naumann and Higgins (2015) found that in *M. rubra*-infested areas, native ant abundance and richness both declined. Verble-Pearson and Pearson (2016) also observed a decline in arboreal invertebrate abundance and the complete absence of arboreal ant species in plots infested by *M. rubra*. However, these results are correlative, and other non-native ant research suggests that negative correlations between native and non-native ants may reflect different habitat preferences more than direct effects (King and Tschinkel 2008). The objective of this study was to use observational surveys and experimental species removal experiments to determine if *M. rubra* directly reduces native ant and non-ant invertebrate communities. Given that non-native ants often become more carnivorous in their invaded range (Gorb and Gorb 1999), and the *M. rubra* populations at Tiff are incredibly dense, I predict that *M. rubra* removal will result in increased native ant and non-ant invertebrate abundance and richness. Additionally, in order to assess the ecosystem impact of *M. rubra*, I predict that *M. rubra* removal will result in increased decomposition with intact invertebrate communities.

Methods

Observational study

Study sites

I surveyed six municipal parks/preserves in Western New York (WNY) to observe differences in native ant and invertebrate populations at sites invaded and uninvaded by *M. rubra*. Three of the parks were heavily invaded by *M. rubra*: Tiff Nature Preserve (Tiff), Times Beach Nature Preserve and Fort Niagara State Park. Tiff is a 108-hectare urban nature preserve located on the eastern shore of Lake Erie. Times Beach is a 20-hectare site that was dredged and used as a dumping site in the 1950s, abandoned, and then repurposed as a nature preserve, and Fort Niagara is a 204-hectare park historically used as a military fort that now contains recreational fields, a nature center, and forested areas with hiking trails. For comparison, I chose the nearest uninvaded park: Red Jacket River Front Park, Earl W. Brydges Artpark State Park, and Darien Lakes State Park. Red Jacket River Front Park is a 1.6-hectare former shipping and industrial site restored to woodland and marsh habitat. Earl W. Bridges Artpark State Park is a 44-hectare park overlooking the Niagara Gorge that contains forested hiking trails and serves as a venue for concerts and other recreational events, and Darien Lakes State Park is a 747-hectare park containing campgrounds, woodlands, streams, hiking trails, and Harlow Lake.

In May 2017, ten 5-m² plots ($n = 60$ plots total) were established at each of the six study sites. The plots were equally spaced at 10-m intervals along 200 m transects that crossed forested areas of the parks/preserves at least 10 m from forest edges. Ten-minute timed surveys were conducted at each plot biweekly from May-September. All rocks, downed wood, and anthropogenic items within each plot were overturned and the invertebrates residing under each were counted and identified to order. Soil moisture measurements were taken at each plot using a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA), and soil temperature was determined using a wide-range thermometer (Taylor

Precision Produces, Las Cruces, NM, USA). These measurements were taken at three random locations within each sampling plot, and the values were averaged.

Experimental study

Study Site

Tifft historically was a shipping center for coal, wood, and iron ore, and a dumping ground for industrial and residential waste, but was turned into a nature preserve in the 1970s (Spiering 2009). The current habitat at Tifft includes woodlands, marshes, grasslands, and ponds. The canopy is dominated by native eastern cottonwood (*Populus deltoides*) and the understory by non-native vegetation, such as Japanese knotweed (*Fallopia japonica*) and buckthorn (*Rhamnus cathartica*) (Spiering 2009, Labatore et al. 2016).

Experimental Plots

In order to test the impacts of *M. rubra* removal, 20 2-m² square plots were used, with 10 plots receiving ant pesticide and 10 plots serving as controls. Based on ant surveys in 1994 and 2015 (Warren et al. in review), experimental and control plots were randomly selected from areas containing approximately equal and high densities of *M. rubra* (>1000 ants plot⁻¹). Each of the twenty plots also contained similar soil temperature and moisture conditions.

Based on an ant-bait design derived from Boser et al. (2012), I used Extinguish Plus [active ingredients: 0.25% s-methoprene (ant toxicant) and 0.36% hydramethylnon (ant growth inhibitor)] coupled with a sugar attractant and deployed in polyvinyl chloride (PVC) bait stations. PVC bait stations were 3.8-cm in diameter and 41-cm in length, capped at both ends,

with small holes on one end to allow entry of ant-sized organisms. I used Extinguish Plus toxicant bait because typical toxic baits are not effective in managing ant populations of species such as *L. humile* and *M. rubra* which transport food through trophallaxis (consumption and regurgitation) (Groden et al. 2007, Boser et al. 2012). These species ingest their food, transport it to the nest, and regurgitate it for the queen and larval consumption (Cassill and Tschinkel 1996). When feeding on a toxic bait, the workers consume the poison and die before reaching the nest or queens. Soybean-encased ant toxicant granules, such as Extinguish Plus, provide a toxicant delivery method designed to target ants that engage in trophallaxis. The ants can consume the granules, which delay the metabolic breakdown of the poison allowing the workers time to engage in trophallaxis and feed the toxicant to the queens (Boser et al. 2012). Since the dominant North American woodland ant, *Aphaenogaster rudis* (King et al. 2013), does not use trophallaxis for feeding (Cassill and Tschinkel 1996) and has been previously observed low abundances in the infested plots along with other non-target species, the non-target effects were expected to be minimal. Additionally, a study conducted by Gaigher et al. (2012) used a pesticide with the same active ingredients as Extinguish Plus and found no non-target impacts.

The PVC bait stations were placed in the center of the 2-m² treatment plots and left for the duration of the experiment. Each bait station was monitored and refilled biweekly May-July 2017. However, 2017 was a particularly wet Summer, and the bait stations appeared ineffective as very few ants entered the PVC and fungal growth quickly built up inside the PVC baits despite biweekly cleaning and refilling. As a result, the pesticide application method was changed to broadcast spreading in the treatment plots following the manufacturers recommendation for imported fire ants (*Invictus solenopsis*, 1.68 kg/ha weekly) for the remainder of the experiment (July-September).

Invertebrate sampling

All invertebrates were sampled biweekly in each plot May – September 2017. In order to augment invertebrate sampling, four 0.25 m x 0.25 m plywood coverboards were placed in each plot at each corner of a 1.5-m² square within the 2-m² plots. Environmental measurements were taken using the same methods as in the observational study.

Leaves of *P. deltooides*, *F. japonica*, and *R. cathartica* were collected (representing the Tift ground cover), mixed thoroughly, cleaned and oven-dried for 48 hours until equilibrium moisture content was reached. Four grams of the dried leaf mix were then placed into 2.5-mm mesh leaf bags with nine 6-mm holes punched into each bag to allow the entry of larger organisms. Four leaf bags were placed in each plot for the duration of the removal experiment. Two leaf bags were placed underneath the plywood coverboards and two leaf bags were placed next to the remaining coverboards. The packs were removed from the study site in early September, rinsed and oven-dried for 48 hours, and re-weighed to determine any loss in dry mass. All invertebrates within the leaf packs were collected and identified.

Data analysis

All statistical analyses were performed using the R statistical program (2017). Models with multiple independent variables were tested for multicollinearity (variance inflation < 2.5) using the 'car' package (Fox and Weisberg 2011) and logistic regression models were tested for overdispersion ($\Phi < 1$).

Native ant, as well as detritivore and predatory invertebrate (Table 1) abundance for each timed survey plot were analyzed as functions of *M. rubra* presence/absence and week (and an

M. rubra x week interaction term) using Generalized Linear Models (GLM) assuming quasi-Poisson error distributions (because the count data were overdispersed) and invertebrate species richness was analyzed using a GLM with Poisson error distribution. Linear regression models were used to evaluate *M. rubra* abundance as a function of temperature and soil moisture (in separate models as these variables often covary).

Myrmica rubra, native ant, detritivore, and predatory invertebrate abundances were analyzed as functions of pesticide treatment and application days using GLMs with quasi-Poisson distributed data fit with Analysis of Deviance (ANODEV) models with an 'F' test.

Myrmica rubra x experimental days interaction terms were included to measure the cumulative effect of repeated pesticide applications.

The difference between initial and final leaf dry mass (i.e. decomposition) was calculated for each sample. Decomposition was analyzed using the 'lme4' package (Bates et al. 2015) and a linear mixed model with cover (coverboard and exposed) and treatment (pesticide and control) as fixed effects and plot as a random effect (to account for pseudoreplication from multiple decomposition bags per plot).

Results

Timed surveys

Native ant abundance was lower where *M. rubra* was present (*coeff.* = -4.404, *SE* = 0.582, *t-value* = -7.570, *p-value* < 0.001) [Figure 1] and decreased throughout the summer (*coeff.* = -0.134, *SE* = 0.040, *t-value* = -3.347, *p-value* < 0.001). An interaction between *M. rubra* presence and study weeks indicated that predatory invertebrate abundance decreased throughout the

summer where *M. rubra* was present (*coeff.* = 0.116, *SE* = 0.049, *z*-value = -2.381, *p*-value = 0.017) [Figure 2A]. Conversely, detritivore abundance was higher where *M. rubra* was present (*coeff.* = 1.552, *SE* = 0.189, *t*-value = 8.179, *p*-value < 0.001) [Figure 2B] but decreased throughout the summer independent of *M. rubra* presence (*coeff.* = -0.100, *SE* = 0.041, *t*-value = -2.442, *p*-value = 0.015). Additionally, detritivore abundance was higher where predatory invertebrate abundance was higher (*coeff.* = 0.123, *SE* = 0.043, *t*-value = 2.830, *p*-value = 0.005). Overall invertebrate taxonomic richness was greater with *M. rubra* presence (*coeff.* = 1.340, *SE* = 0.171, *t*-value = 7.828, *p*-value < 0.001), and sites where *M. rubra* was present had both higher soil moisture (*coeff.* = 0.135, *SE* = 0.014, *t*-value = 9.308, *p*-value < 0.001) [Figure 3A] and higher temperatures (*coeff.* = 0.193, *SE* = 0.052, *t*-value = 3.690, *p*-value < 0.001) [Figure 3B].

Myrmica rubra removal

The pesticide treatment decreased *M. rubra* forager abundance by 44% (untreated = 129.6 *M. rubra* ants plot⁻¹; treated = 72.4 *M. rubra* ants plot⁻¹) by the end of the study. A treatment x experimental days interaction indicated that the effectiveness of the pesticide treatment in decreasing *M. rubra* foragers increased with experimental days (*Df* = 1, *Dev.* = 535, *Res. Df* = 136, *Res. Dev.* = 8724, *F*-value = 6.107, *p*-value = 0.015) [Figure 4]. Detritivores decreased in abundance with experimental days in *M. rubra* removal treatment plots (*Df* = 1, *Dev.* = 559, *Res. Df* = 136, *Res. Dev.* = 16850, *F*-value = 3.859, *p*-value = 0.052) [Figure 5A]. Conversely, the abundance of predators increased with experimental days and *M. rubra* removal (*Df* = 1, *Dev.* = 11.6, *Res. Df* = 138, *Res. Dev.* = 252, *F*-value = 3.14, *p*-value = 0.009) [Figure 5B]. Overall invertebrate taxonomic richness increased from 4.25±0.2 to 4.95±0.2 taxonomic units plot⁻¹ with

M. rubra removal ($Df = 1$, $Dev. = 3.7$, $Res. Df = 138$, $Res. Dev. = 82$, $F\text{-value} = 6.63$, $p\text{-value} = 0.011$).

Native ant abundance increased with pesticide treatment ($Df = 1$, $Dev. = 97.0$, $Res. Df = 138$, $Res. Dev. = 389$, $p\text{-value} < 0.001$) [Figure 6] and somewhat with the number of days after treatment initiation ($Df = 1$, $Dev. = 23.7$, $Res. Df = 137$, $Res. Dev. = 365$, $p\text{-value} = 0.08$).

Indeed, native ant colonies only appeared in the removal plots approximately 40 days after treatments were initiated, and no native ants were found in any untreated plot at any point in the study (untreated = 0 native ants plot⁻¹; treated = 7 native ants plot⁻¹).

Leaf decomposition

Leaf litter decomposition was unaffected by the pesticide treatment ($coeff. = -0.375$, $SE = 0.390$, $t\text{-value} = -0.958$, $p\text{-value} = 0.352$) and *M. rubra* abundance ($coeff. = -0.039$, $SE = 0.089$, $t\text{-value} = 0.445$, $p\text{-value} = 0.657$). Leaf litter decomposition was higher below coverboards ($coeff. = -0.776$, $SE = 0.331$, $t\text{-value} = -2.344$, $p\text{-value} = 0.022$) and somewhat greater with the total number of invertebrates found in the leaf bags ($coeff. = 0.029$, $SE = 0.018$, $t\text{-value} = 1.617$, $p\text{-value} = 0.110$). Invertebrates were more common in leaf bags under the coverboards (14.7 ± 1.91) than leaf bags outside the coverboards (7.00 ± 0.87 ; $p\text{-value} < 0.001$).

Discussion

A consistent, negative relationship was found between *M. rubra* and native ants throughout this study. In the observational study, native ants were more abundant in the uninvaded parks, suggesting that *M. rubra* either displaces native ants or there are habitat differences that

segregate *M. rubra* and native ants. However, field experiments revealed a one-way, negative relationship between *M. rubra* and native ants, as native ants rebounded only in the plots where *M. rubra* was removed, suggesting that *M. rubra* directly limits native ant populations. The relationship between *M. rubra* and non-ant invertebrates also was consistent between the observational and experimental portions of the study as detritivores increased with *M. rubra* and predatory invertebrates either decreased or were unaffected. Leaf decomposition appeared to be unaffected by *M. rubra* presence but was greater under coverboards as was the number of invertebrates found in leaf bags. Terrestrial decomposition is primarily driven by fungi and is typically slow with very little loss in dry mass after only three months (Voriskova' and Baldrian 2013), indicating that this short study period may have been insufficient to determine potential decomposition impacts of *M. rubra* removal.

Negative relationships are often observed between native and non-native ant species. Observational studies on species such as *Linepithema humile* (Kennedy 1998, Holway and Suarez 2006) and *Solenopsis invicta* (Morris and Steigman 1993) suggest that these non-natives negatively correlate with native ant populations, though each is inconclusive about the mechanisms driving these relationships. *Myrmica rubra* also appear to negatively correlate with native ants, as Garnas (2004) found only a quarter of the native ant taxa in *M. rubra*-invaded areas as in uninvaded areas, and Garnas et al. (2014) also found fewer native ants where *M. rubra* was present, just as in both portions of my study. Habitat segregation might account for the observed differences between native and non-native ant abundance, as some non-native ants do well in disturbed habitat where natives generally do not (King and Tschinkel 2008, Michlewicz and Tryjanowski 2017), and abiotic factors have been found to play a role in both ant invasions (Menke and Holway 2006) and observed differences between native and non-native ant

abundance (Stuble et al. 2009). Alternatively, non-native ants are thought to be superior competitors to native ant species, both for food resources (Porter and Savignano 1990, Human and Gordon 1996, Garnas et al. 2014) and nest space (Holway et al. 2002), actively establishing their dominance of invaded habitats. Species such as *L. humile*, *S. invicta*, and *M. rubra* use a polygyne, unicolonial structure to rapidly expand their populations (Porter and Savignano 1990, Human and Gordon 1996, Groden et al. 2005) which may ultimately lead to a competitive numerical advantage over smaller ant colonies (Holway et al. 2002). Due to the comparative nature of observational studies, it can be difficult to determine whether the observed inverse relationships between native and non-native ants, such as *M. rubra*, are a result of habitat segregation or non-native ant dominance.

A more direct approach to studying non-native species impacts is the use of experimental eradication (Zavaleta et al. 2001, Zarnetske et al. 2010, Simberloff et al. 2013) which allows for comparison within an invaded area and the subsequent elimination of problematic confounding factors associated with observational studies. Recently, experimental methods also have been applied to invasive ant management (Boser et al. 2012), such as the ant-addition experiment implemented by King and Tschinkel (2008) which suggests that *S. invicta* invasion is driven by habitat conditions and therefore does not actively induce a decline in native ant abundance. To my knowledge, my study is the first to use removal methods to eradicate *M. rubra* from an invaded area, and despite possible reduced impacts due to the rainy summer season, the pesticide treatment significantly reduced *M. rubra* populations, which was sufficient to determine that *M. rubra* abundance, rather than habitat, limits native ants. As such, the results of my experimental removal study, in contrast to King and Tschinkel (2008), suggest that *M. rubra* is actively

limiting native ant populations in Tiffit, as native ants were able to rebound once *M. rubra* were reduced.

Two native species, *Crematogaster cerasi* and *Temnothorax longispinosus*, appeared in the pesticide-treated plots once *M. rubra* populations had decreased. *Temnothorax longispinosus* is a native ant that nests in plant and rock cavities, forms small colonies (Herbers 1986), and has not been documented as an aggressive species (Snelling et al. 2014). *Temnothorax* ants typically forage for small invertebrates such as collembolans (Bengston and Dornhaus 2013) and are therefore unlikely to consume the pesticide granules used in this study. *Crematogaster* are relatively aggressive, arboreal ants that actively hunt invertebrate prey on trees and plant material (Richard et al. 2001, Longino 2003), making them less susceptible to the ground-administered pesticide. As *M. rubra* ants also forage in trees, they may be competing with *C. cerasi* and other arboreal invertebrates for resources (Verble-Pearson and Pearson 2016). However, given that Warren et al. (in review) found *M. rubra* to be less competitive for food resources and less directly aggressive than native ants, it is unlikely that *M. rubra* are displacing native ants via competitive abilities alone. Rather, priority effects coupled with supercolony characteristics may have allowed the initial *M. rubra* population to obtain optimal nest spaces and grow large enough to compensate for their lesser competitive and aggressive tendencies against native ants. In a follow-up study to Porter and Savignano (1990), Morrison (2002) observed that a native invertebrate community may be able to rebound naturally following the initial invasion period of a non-native ant. However, *M. rubra* has persisted in Tiffit since the 1970's (Warren et al. in review), thus a rebound by native ants seems unlikely without management intervention.

In contrast to the native ants, non-ant invertebrate abundance positively correlated with *M. rubra* abundance in the observational portion of this study. Many studies have observed no

significant associations (Holway 1998a, Hanna et al. 2015) and even positive associations (Morrison and Porter 2003) between non-native ants, such as *S. invicta* and *L. humile*, and non-ant invertebrate communities. Additionally, a positive association between *M. rubra* and non-ant invertebrates has been observed in at least one other observational study (Garnas 2004), and shared habitat or microhabitat preferences may account for these positive correlations (Morrison and Porter 2003) as the habitat requirements for *M. rubra* and ground-dwelling invertebrates, such as isopods, often overlap (Garnas 2004). Although these observational results are inconsistent with some of the existing literature (Porter and Sauvignano 1990, Naumann and Higgins 2015), the experimental portion of this study also suggested that detritivores may benefit from *M. rubra* invasion, as the non-treatment control plots contained fewer predator invertebrates and higher prey species abundances. Positive relationships between non-native ants and detritivores coupled with negative relationships between predators and non-native ants have been observed previously (Krushelnycky and Gillespie 2008), though my study is the first to my knowledge to provide experimental evidence for such relationships with *M. rubra*. Experimental evidence also exists for negative relationships between non-native fire ants and predators that typically feed on invertebrates, such as birds and rodents (Pedersen et al. 2003, Allen et al. 2004). Although the experimental results suggest a positive impact of *M. rubra* on detritivores, a positive relationship between detritivores and predators was found in the observational study as well. Therefore, *M. rubra* is likely not benefiting detritivore abundance by outcompeting predatory invertebrates but instead may be keeping larger vertebrate predators out of infested sites (Pedersen et al. 2003) and allowing invertebrates to thrive in habitat with limited larger predators.

These results suggest *M. rubra* is actively influencing invertebrate communities at invaded locations in Western New York. The prior arrival of *M. rubra* at Tiffit coupled with their supercolony structure and successful, invasive characteristics, may allow *M. rubra* to exclude native ants, and therefore, the eradication of *M. rubra* from Tiffit may allow the native ant community to expand and use the nest space currently exploited by non-natives. However, management efforts may also negatively impact local non-ant invertebrates as *M. rubra* appear to be beneficial to the detritivore invertebrate community.

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Predatory Invertebrates	Detritivore Invertebrates
Order: Coleoptera	Order: Diplopoda
Order: Chilopoda	Order: Isopoda
Class: Arachnida	Class: Clitellata
	Class: Collembola
	Class: Gastropoda

Table 1. List of taxonomic units and their assigned functional groups.

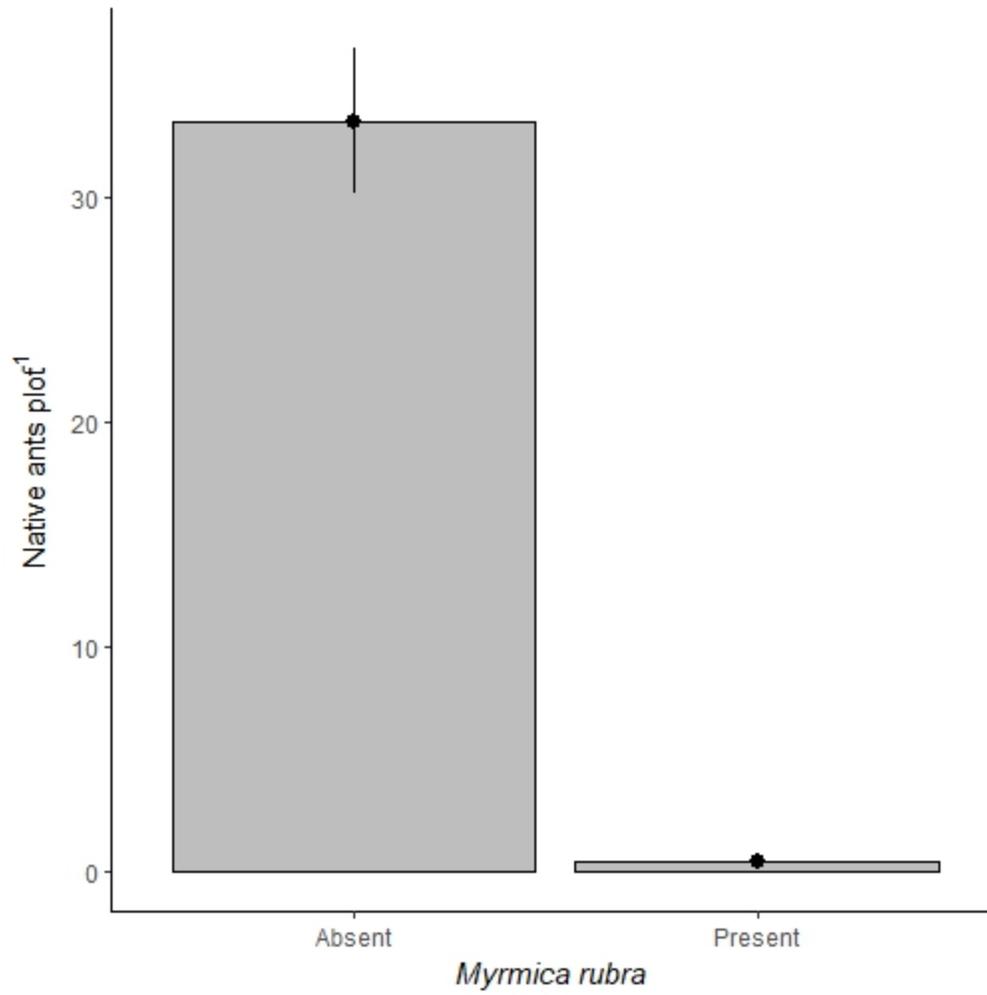


Figure 1. Native ant abundance versus *Myrmica rubra* presence in six parks across Western New York. Native ant abundance per plot was greater where *M. rubra* was absent.

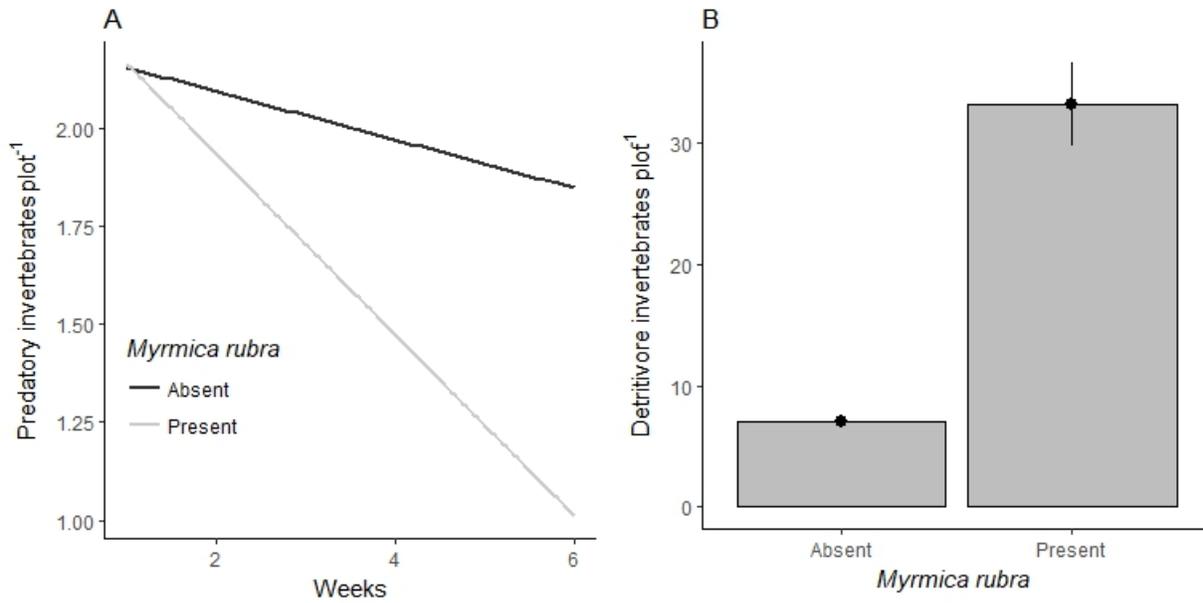


Figure 2. Predatory invertebrate abundance (a) and detritivore invertebrate abundance (b) as a function of *Myrmica rubra* presence in six parks across Western New York. Predatory invertebrates declined throughout the summer where *M. rubra* was present and remained relatively unchanged where *M. rubra* was absent. Greater detritivore abundance was found in the presence of *M. rubra*.

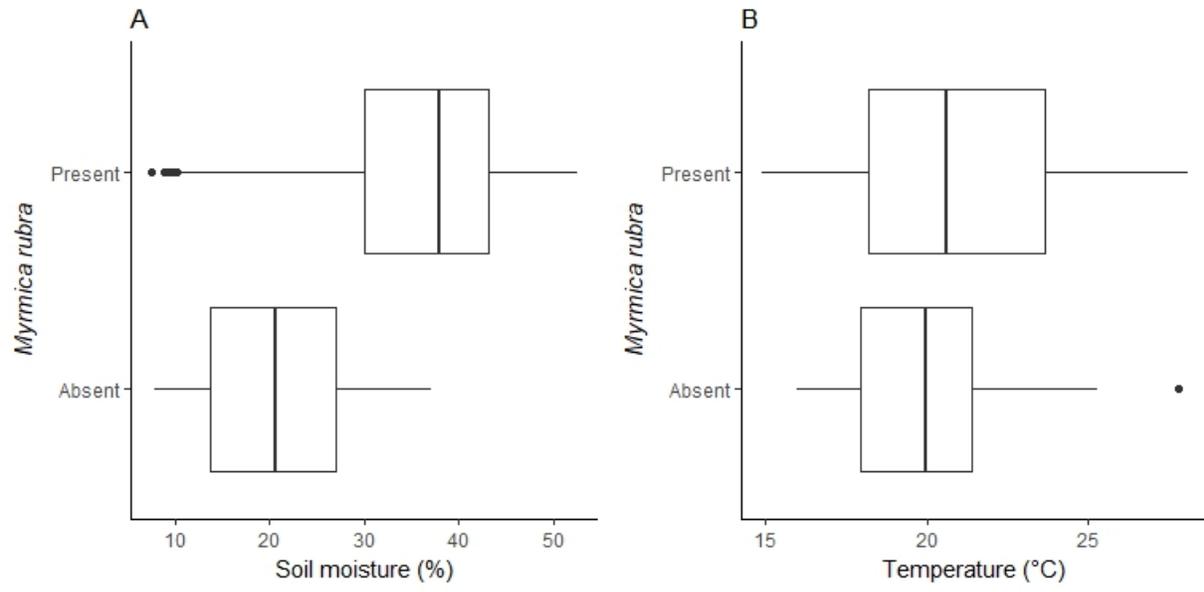


Figure 3. Observed *Myrmica rubra* presence as a function of (a) soil moisture and (b) temperature in six parks across Western New York. *Myrmica rubra* was present at higher soil moisture and warmer temperature conditions.

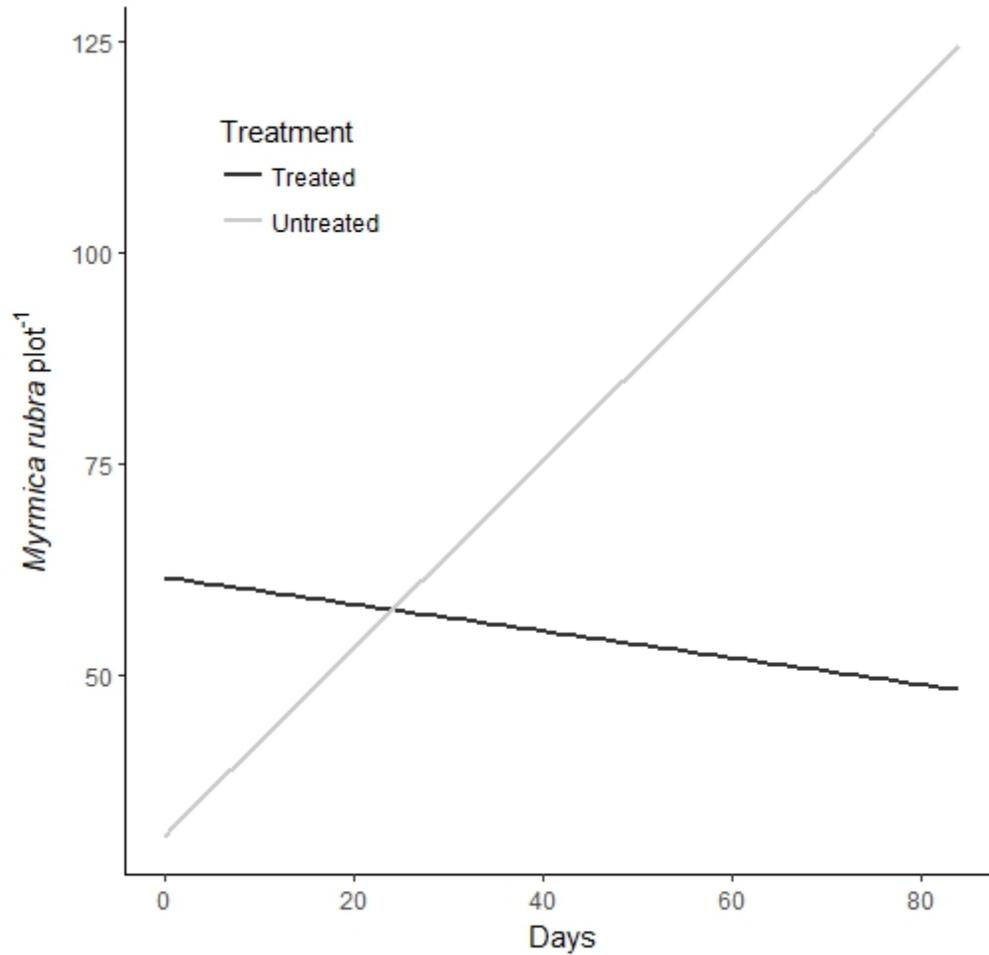


Figure 4. Interaction plot for treatment x days impacts on *Myrmica rubra* abundance using a pesticide treatment at Tift Nature Preserve. A significant interaction between treatment and days indicated that the pesticide treatment became more effective at reducing *M. rubra* populations in pesticide-treated plots as time went on.

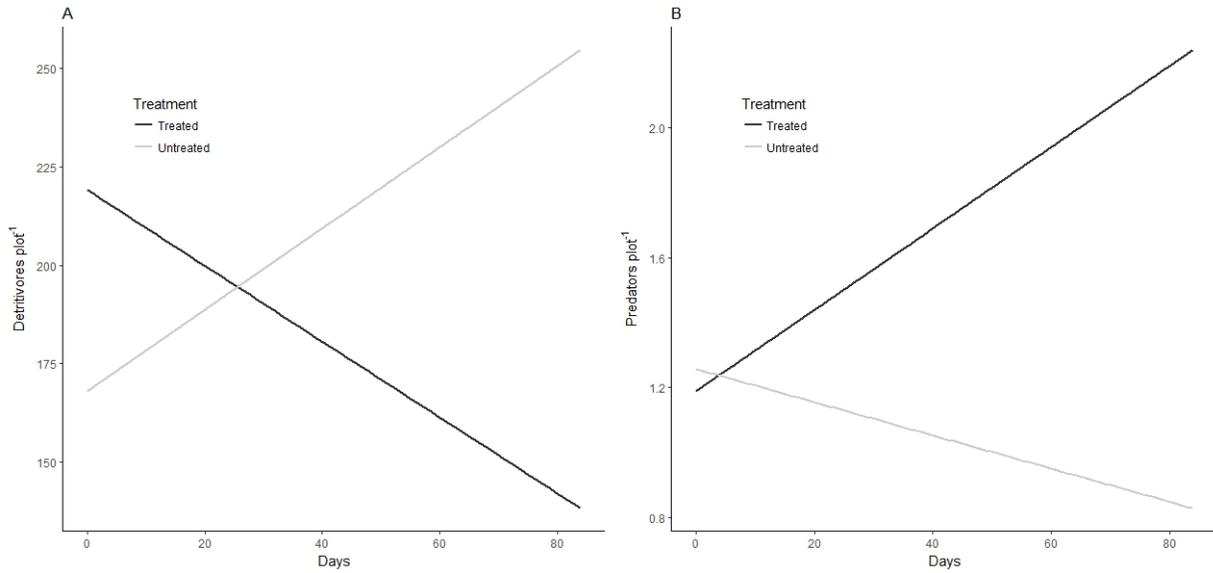


Figure 5. Interaction plots for treatment x days impacts on (A) detritivores and (B) predator invertebrates using a pesticide treatment at Tiff. Significant interactions indicated both a decrease in detritivores and an increase in predator invertebrates in pesticide-treated plots as time went on.

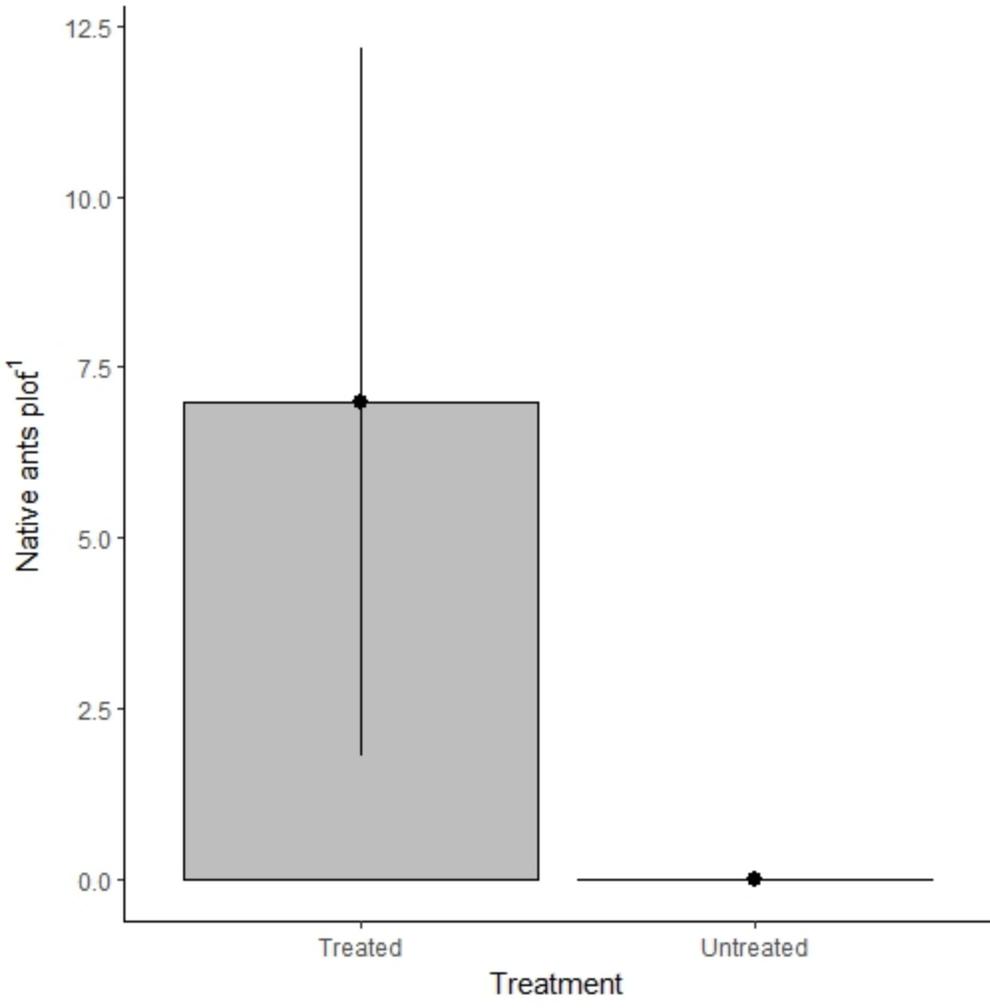


Figure 6. Pesticide treatment impact on the average number of native ants per plot at Tifft. The average number of native ants in untreated plots was 0 ants per plot and 7.00 ± 5.17 ants per plot in pesticide-treated plots. No native ants were found in any control plots throughout the study.