

**What ignites fire ant density and impacts in longleaf pine ecosystems?**

by

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## *Abstract*

Invasive invertebrates are studied due to their impacts on human and ecosystem health, but impacts on native invertebrates are less known. The red imported fire ant (RIFA, *Solenopsis invicta*) is an ideal model species to quantify this relationship as they take advantage of disturbed landscapes, which is problematic for disturbance-mediated longleaf pine ecosystems (*Pinus palustris*) of the southeastern United States. I hypothesized that RIFA mound numbers are driven by environmental variables (e.g., prescribed fire, region, disturbance history) in longleaf pine ecosystems, and that higher RIFA presence would decrease native and increase non-native ant species richness. I tested these hypotheses on 11 properties in Florida and Georgia, and results indicated that RIFA mound numbers do relate to certain environmental variables and higher RIFA presence did decrease native and increase non-native ant species richness. My findings can help land managers in balancing costs of invasive species control and meeting conservation goals.

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## List of Abbreviations

GPS      Global positioning system

RIFA     Red imported fire ants

## Chapter 1: Introduction

One of the greatest threats to conservation worldwide is the spread of invasive species, which impact native species and ecosystems through predation, habitat destruction, and competition (MEA 2005). While \$128 billion is spent annually in the US to mitigate their economic damage (Pejchar and Mooney 2009), invasive species incur additional costs through animal extinctions (Clavero and García-Berthou 2005), decreasing biodiversity, and impairment of ecosystem services (Pejchar and Mooney 2009, Pyšek and Richardson 2010). As a result, preventing the establishment and spread of invasive species, evaluating their effects on ecosystems, and determining appropriate management responses to invasion are serious priorities for land managers globally (Lowry et al. 2013).

An area of concern that is poorly understood is how restoration of natural disturbance regimes may influence biological invasions and their subsequent impacts on native species. For example, prescribed burning is a common practice to promote longleaf pine savannas in the southeastern United States, both on old field sites (historically agricultural) and on sites dominated by native groundcover that have never been cultivated. Many species directly benefit from maintenance of these ecosystems, and prescribed burning is an essential component of reversing declines in grassland species such as the federally endangered red-cockaded woodpecker (*Picoides borealis*), indigo snake (*Drymarchon couperi*), and gopher tortoise (*Gopherus polyphemus*).

However, invasive species may also take advantage of these management practices and have negative impacts on species of conservation concern. A prime example of an invasive species expanding in the face of restoration efforts is the red imported fire ant (*Solenopsis invicta*, hereafter RIFA). Native to South America, RIFA was introduced into the US between the 1930s and 1940s (Callcott 2002). RIFA take advantage of disturbed areas (e.g., pastures, mowed areas near roads) to develop new colonies and expand their range each year, altering community composition and ecosystem integrity (Tschinkel 1988, Camilo and Phillips 1990, Plowes et al. 2007). The species is now established in over 128 million ha in the US (Morrison et al. 2004, Zhang et al. 2007). Under current climatic conditions, RIFAs have the potential to continue expanding their US distribution northward (Korzukhin et al. 2001, Morrison et al. 2004), with even further expansions possible due to climate change (Morrison et al. 2005). This historical establishment and continued expansion of RIFA is of high concern for conservation efforts. RIFA reach high densities, are highly aggressive, and are omnivorous, giving them potential to impact agricultural crops (Jetter et al. 2002), invertebrates, and vertebrates including herpetofauna, mammals, and birds (Allen et al. 2001, Ferris et al. 1998, Reagan et al. 2000). Among vertebrate wildlife species, grassland birds may be at risk of negative population-level effects of RIFA predation as this guild of birds has already been in steep decline for decades (Brennan 1991, Wojcik et al. 2001).

The severity of impacts RIFA have on a system (Macom and Porter 1996) can vary. For instance, RIFA depredate a number of altricial species, including northern bobwhite quail (*Colinus virginianus*, hereafter bobwhite) and the American alligator (*Alligator mississippiensis*, Reagan et al. 2000), as well as some precocial species like the loggerhead turtle (*Caretta caretta*, Allen et al. 2001a). Previous research found that that region partially explained variation in RIFA

nest depredation of bobwhites, but did not clarify what regional factors were influential RIFA (Haines et al. 2017). This uncertainty reduces the ability of managers to identify the conditions (i.e. when and where) under which RIFA effects on native species warrant higher concern.

Environmental factors such as site disturbance history, hydrology, and climate are known to affect RIFA occurrence and activity (Porter and Tschinkel 1987, Tschinkel 1988, Korzukhin et al. 2001). Soil type could be important due RIFAs reliance on underground nests and foraging tunnels, but there is currently a debate in the literature on this topic. Some studies have found no evidence that soil type impacts RIFA (Wangberg et al. 1980, Porter et al. 1991), but others suggest that soil characteristics have significant influence, such as particle size, bulk density, and soil moisture (Ali et al. 1986). Testing soil in relation to other environmental and management factors could shed light on this debated topic. Furthermore, there has been minimal work done comparing RIFA densities between old-field and native groundcover, as historical disturbance may impact present day invasions (Forbes et al. 2002).

RIFA provide a model taxon for assessing the basic question of how habitat and disturbance (e.g., land use, wildfire) interact with biological invasions and subsequent nest predation rates on grassland birds. Because little is known about the interactions of environmental characteristics and land management on RIFA, my study will provide information for managers to address this problem. My goal is to determine not only which environmental variables impact RIFA, but also how RIFA are impacting their environment.

To that effect, I will first test what environmental variables influence RIFA mound numbers. My first hypothesis is that RIFA mound density is driven by soil type, groundcover type, and burn interval. After evaluating the relationship of RIFA mound number to variables of interest, I will also determine how RIFA numbers influence native and non-native ant species

richness to model how RIFA are impacting native invertebrates. Specifically, my second hypothesis is that as RIFA numbers increase, native ant species richness will decrease while non-native ant species richness will increase. Answering my two hypotheses could enable land managers to control RIFA in specific areas where the risk of RIFA impact is highest, allowing them to cut down on costs while attaining their conservation goals. On a larger scale, this work fills a gap in understanding how RIFA invasions may be related to restoration and disturbance, which can help untangle basic biological invasion questions and help guide management and habitat improvement efforts to protect native early-successional species which benefit ecosystem health and stakeholders.

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**Chapter 2: Interactions of prescribed fire, soil, and fire ants: the burning question.\***

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## *Abstract*

Red imported fire ants (*Solenopsis invicta*, hereafter RIFA) are an aggressive invasive species expanding in the face of disturbance-mediated ecosystem restoration efforts (e.g., prescribed fire). Land managers are concerned habitat restoration may increase RIFA abundance and negatively impact species of conservation concern. I hypothesized that RIFA mound numbers correlated with burn interval, groundcover type, and soil type. I assessed my hypothesis by surveying 11 properties in Georgia and Florida during 2016 and 2017. Plots were randomly selected and characterized by burn rotation (burned or unburned within a year), groundcover (native or old field), and soil characteristics. The top Poisson model suggests that year, region, burn interval, and soil pH influence RIFA mound numbers. These variables could influence other invasive invertebrates, and correlate with past research investigating variation in RIFA nest depredation. Quantifying the indirect variables influencing RIFAs and other invasive invertebrates will help land managers make informed management decisions for conservation efforts.

**Keywords:** distance sampling, habitat selection, pine savanna, *Solenopsis invicta*

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One of the greatest threats to conservation worldwide is the spread of invasive species, which impact native species and ecosystems through predation (Johnson 1961), habitat destruction (Allen et al. 2004), and competition (MEA 2005). In the US, invasive species cause an estimated \$120 billion in damage and control efforts each year (Pimentel et al. 2005) on top of the ecological and economic costs incurred by increasing animal extinctions (Clavero and García-Berthou 2005), decreasing biodiversity (Wojcik et al. 2001), and impairing ecosystem services (Pejchar and Mooney 2009, Pyšek and Richardson 2010). As a result, preventing the establishment and spread of invasive species, evaluating their effects on ecosystems, and determining how management practices affect invasion are a priority for land managers (Lowry et al. 2013).

Certain types of management may facilitate invasion (Jetter et al. 2002), and it is poorly understood how restoration of natural disturbance regimes may influence biological invasions, as well as the subsequent impacts on native species. For example, prescribed burning is a common practice to restore and promote different types of early successional landscapes in the US (Forbes et al. 2000, Williamson et al. 2002). Restoration of early successional habitat is critical in a number of locations as species that depend on it have been declining in many locations (Van Lear et al. 2005). These species, including federally threatened and endangered species, directly benefit from maintenance of early successional ecosystems (Wilson et al. 1995, Palmer et al. 2012). However, invasive species may also take advantage of disturbance-mediated management. For instance, ponderosa pine (*Pinus ponderosa*) forests of the Western US have been rapidly invaded by cheatgrass (*Bromus tectorum*) following the use of fire as cheatgrass is able to grow back faster than native grasses (Kerns et al. 2006). Notably, however, increases in invasive species are not universal as species vary in their response to disturbance.

Disturbance is just one of multiple environmental factors that can influence the presence and success of invasive species on a landscape (Tschinkel 1998). Other factors include direct variables (e.g., land use and disturbance events) and indirect variables (e.g., site disturbance history, climate, and local animal and plant communities; Porter and Tschinkel 1987, Tschinkel 1988, Korzukhin et al. 2001). Differentiating the effects of some environmental variables is difficult, as they can be confounded by interactions (Beketov and Liess 2008). Testing variables of potential biological significance in relation to each other and management practices could provide information to improve management.

Red imported fire ants (*Solenopsis invicta*; hereafter, RIFA) provide a model taxon for assessing of how different environmental variables, such as land cover, disturbance regimes, and soil characteristics, interact with an invasive species and their subsequent impacts on native fauna. RIFA are generalist foragers that readily colonize disturbed areas (Tschinkel 1988), and their abundance is likely linked to depredation rates on ground nesting species, such as northern bobwhite quail (*Colinus virginianus*; Mueller et al. 1999, Dabbert et al. 2002, Haines et al. 2017). However, considerable uncertainty remains about long-term rates of RIFA-caused mortality and competition at various life stages. This uncertainty reduces the ability of managers to identify the conditions (i.e. when and where) under which RIFA depredation warrants higher concern. While some research exists on the effect of prescribed burning on RIFA abundance and distribution (Forbes 2002), it has not focused on areas with decades of burn history. Furthermore, RIFA depredation rates can vary markedly between landscapes that are similarly managed with prescribed burning (Haines et al. 2017). These results suggest that there are other factors influencing RIFA presence and depredation, such as soil properties and site disturbance history (Keeley 2005).

Given the lack of understanding about how environmental variables affect the presence and success of invasive species, the overarching goal of my research is to quantify which variables have the largest influence on RIFA. A commonly used indicator of RIFA presence and density in past research is RIFA mound number. Therefore, I hypothesize that RIFA mound density is driven by soil type, groundcover type, and burn interval. From my hypothesis, I had three predictions. Specifically, I predicted that RIFA mound numbers and density will increase as sand content increases and bulk density decreases. This prediction is based on research indicating that properties with sandier, looser soil experiences higher rates of RIFA depredation in quail nests (Haines et al. 2017). Additionally, properties with old field (historically agricultural) groundcover are predicted to have a higher number and density of RIFA mounds than properties where native groundcover has been preserved, as areas of old field groundcover tend to have a higher number of non-native or invasive species present (Keeley 2005). I also predict that areas burned within a survey year will increase RIFA mound numbers and overall density when compared to areas not burned during the survey year (number of mounds/ha). This third prediction is based on the tendency of RIFAs to colonize disturbed areas (Tschinkel 1988) and past research on their relationship with prescribed fire (Forbes 2002).

## **Methods**

### *Study Area*

I evaluated RIFA presence on 11 properties in two study regions in the southeastern US (Figure 2.1). One region is in Baker and Dougherty counties in southwest Georgia (hereafter, Albany region), and the other in Leon and Jefferson counties near the Georgia/Florida border (hereafter, Tallahassee region). In the Albany region, I surveyed three hunting properties with old field groundcover, embedded in a 120,000 ha landscape of similar properties. These

properties consist of low basal area (9.2–13.8 m<sup>2</sup> per ha), old field pine forests in an open pine-grassland structure maintained through commercial thinning and prescribed fire, with small fallow fields throughout the area (Palmer et al. 2012). The majority of trees are longleaf pine (*Pinus palustris*) and slash pine (*P. elliottii*), with scattered hardwoods such as live oak (*Quercus virginia*), southern red oak (*Q. falcata*), and water oak (*Q. nigra*). Herbaceous cover is predominantly warm season grasses, such as broomsedge (*Andropogon* sp.), annual broad-leaved forbs, and legumes (Burger et al. 1998). These three old field properties in the Albany region were converted to agricultural fields in the 1800s, but after agriculture was abandoned in the 1900s these lands were seeded back to pine and native vegetation maintained by prescribed fire. Also in the Albany region are two properties with native groundcover (predominately mature longleaf pine and wiregrass (*Aristida stricta*)), specifically in the Dougherty and Worth counties.

The average growing season for the Albany region during this study was mid-March to the end of November, with an average temperature of 24.4° C (NOAA, Weather Underground). The average annual precipitation for Albany was 127 cm, with an average of about 69 cm during the May-August field season (NOAA, Weather Underground). Topography on all Albany properties is relatively flat with few to no hardwood drains.

In the Tallahassee Region, I surveyed three properties with old field groundcover in Leon and Jefferson counties near the city of Tallahassee, Florida. The two old field properties in Leon county are embedded in an approximately 161,874 ha landscape of bobwhite management properties. The property in Jefferson County is approximately 3,682 ha surrounded by properties of similar land management. All three old field properties consist of old field pine forests, mostly loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), interspersed with hardwood drains, hammocks, and small fallow fields. Pine forests are maintained for an open pine-grassland



structure through prescribed fire. Herbaceous groundcover is a mix of warm season grasses, legumes, and forbs (Hammond 2001). Also in the Tallahassee region are four properties with native groundcover (predominately mature longleaf pine and wiregrass), specifically in Thomas county, Georgia, and Jefferson county, Florida.

The average growing season for the Tallahassee region was mid-March to the end of October. The counties around Tallahassee had an average temperature of 25.6° C and an average annual precipitation of 158 cm, with an average of about 66 cm during the May-August field season (NOAA, Weather Underground).

All properties are similarly managed with prescribed fire, typically occurring in March and April of each year. Old field properties burn on a rotation, with managers burning ~50 - 70% of the property and then burning the unburned area the following year (Palmer et al. 2012). Properties with native groundcover varied, most being burned on a similar rotation to the old field properties. However, two native groundcover properties are burned completely each year (properties RH4 and RH5, see Table 2.1).

Soils on the Albany properties are classified as Orangeburg-Lucy-Grady and Norfolk-Wagram-Grady soil associations, which are predominantly sandy-loam textured soils with moderate permeability and low natural fertility (Palmer et al. 2012). Soils in the Tallahassee region are of the Fuquay-Orangeburg-Faceville soil association, characterized by well drained, moderately fertile fine-loam soils with varying amounts of sand and clay (Palmer et al. 2012). The Orangeburg series is common in both the Albany and Tallahassee regions, but otherwise there are no shared soil families, meaning soils between regions vary in characteristics like horizonation, mineral composition, and permeability.

#### *RIFA Surveys*

On each of six properties in the Albany region and five properties in the Tallahassee Region, I randomly sampled six plots (50 × 50 m each, Figure 2.2). Of the 11 total properties, 8 were sampled in 2016 and 3 were added in 2017 (plots: 2016 n = 60, 2017 n = 78, Table 2.1). In areas with two burn types, I surveyed three burned and three unburned plots per property (2016: burned n = 36, unburned n = 24; 2017: burned n = 44, unburned n = 34). Burned plots had been burned during March or April of the survey year, while unburned plots were last burned March or April of the previous year. Because I sampled for two consecutive years, most of the initially burned plots in 2016 became unburned plots in 2017. To choose study plots, I generated 100 random points on property shapefiles in ArcGIS (ESRI 2016), then selected the first three points in burned and unburned areas that were 50 m from known roadways. Old field properties (~9 ha) have annual burns in the spring on a rotating schedule, allowing both burned and unburned areas to be sampled. The native ground properties (~10.5 ha) serve as an example of less disturbed landscapes, as they have minimal sources of disturbance beyond prescribed fire.

Ant mound counts were recorded in plots once per year from May-August in 2016 and 2017. Inside plots, I established six 50 m transects per plot (Forbes et al. 2000), 10 m apart and oriented north to south (Figure 2.3). While randomly placed, the edges of plots were all roughly 50 m away from any road-ways to reduce the possibility of disturbance impact of roads (Forbes et al. 2000). Once the outline of the plot was flagged, an observer walked transects and searched for mounds that were within 5 m of transects. When located, a mound was tested for occupancy by probing the top several times. If ants swarmed, they were examined to determine species. Mounds of RIFA were marked as active, measurements were taken for mound dimensions and perpendicular distance (m) from transect, and GPS coordinates were gathered using a Trimble GEO Explorer 7x unit with 1 - 100 cm accuracy. GPS coordinates for the corners of plots were

also recorded so that surveys could be repeated in the same areas (on a different burn interval) in both years. The mound dimensions were also measured and recorded to the nearest cm.

### *Environmental Variables*

During 2017, I evaluated canopy closure from the center of the plot were determined with a canopy densitometer. I also collected soil cores from a subset of randomly selected plots (n = 50), using both a soil auger and a bulk density probe at the depths of 15 - 25 cm and 40 - 60 cm. The first depth was selected based on the depth RIFA make their forager tunnels (Tschinkel 2006). The second depth was commonly where clay horizonation began for soils in the area and influences moisture retention of the soil, a quality known to influence RIFA (Korzukhin et al. 2001). For each plot, two independent samples were taken at both depths. The independent samples were homogenized with a mortar and pestle, then combined to make a representative sample for their respective plots. Soil samples were then analyzed by the Auburn Cooperative Extension Soil Testing Laboratory to determine pH and particle size (Gee and Bauder 1986). Bulk density samples gathered in the same way as the previous soil samples, but were dried and weighed to determine bulk density for plots (McKenzie et al. 2002). Property disturbance level was also categorized into low, moderate, and high levels by percentage of disking and agricultural land use according to management records and satellite data.

### *Data Analysis*

All analyses were performed in R (R Core Team 2018). Before exploring which variables could be impacting RIFA mound abundance, I first investigated whether I could adequately test my hypotheses using raw mound counts per plot as my response variable. Using standard distance-sampling models (Buckland et al 2012) in package *distance*, I first examined whether detection probabilities (specifically the probability of detecting a mound as a function of its

distance from the closest transect line) varied systematically with factors of interest. Distance analysis (Appendix 1) indicated that detection probability varied between years and increased with increasing mound height. . However, detection did not vary with groundcover, burn interval, or canopy closure. Therefore, I used mound counts as my response variable in later models to avoid the additional complexity of simultaneously modeling detection probability and factors affecting mound density in an integrated analysis (Buckland et al. 2009, Oedekoven et al. 2014).

To quantify the relationship of variables to RIFA mound counts, I ran generalized linear mixed effects models with a Poisson distribution and log link (Bates et al. 2015). In a preliminary analysis, I examined whether mound counts varied within each survey season by fitting models with an effect of Julian date or an interaction of year  $\times$  Julian date. Neither Julian date nor its interaction with year were significant, and thus Julian date was not considered further. I then performed two sets of analyses. The first set used mound counts from all plots and omitted all soil variables. The random effects were individual property and plot, with the fixed effects of region, year, canopy closure, burn interval, groundcover, and disturbance level. Four two-way interactions were included in a preliminary full model because of hypothesized biological importance: year with groundcover, burn interval, and canopy closure, and burn interval with groundcover (code in Appendix 2). To reduce model complexity, I fit a full model with all main effects and the four interactions, and then removed any interactions with  $p > 0.15$  (Harrell 2001). I report Type II tests of significance for the resulting final model (Table 2.2), and provide parameter estimates scaled as overall or year-specific proportional effects on expected abundance. Based on low occurrence of zero counts in my data set and low overdispersion

(overdispersion = 1.15 for full model), I did not examine zero-inflated or negative-binomial models.

My second set of analyses integrated soil covariates with the other variables. Because soil samples were collected from a subset of total survey plots, I used the final model from the first set of analyses, and refit that model to data from the subset of plots where soil was measured. I added one soil variable at a time to that full model and assessed the corresponding parameter estimate and statistical significance for that variable's effect.

## RESULTS

In 2016, 191 total RIFA mounds were found (burned  $n = 86$ , unburned  $n = 105$ ), and in the following year 266 total RIFA mounds were found (burned  $n = 147$ , unburned  $n = 119$ ). Of the four two-way interactions considered in the full model, none were retained (Table 2.2).

Ignoring interactions, overall expected RIFA mound counts in 2016 were 0.96 [ $e^{\beta} = 1.83, (0.786, 1.19)$ ] times the expected count in 2017. The main effect of region indicated 0.58 [ $e^{\beta} = 0.580, (0.339, 0.967)$ ] times the expected RIFA mound counts in Albany than in Tallahassee (Figure 2.5). Pooled across years, the overall main effect of burn type estimated 62% [ $e^{\beta} = 1.62, (1.07, 3.78)$ ] higher expected RIFA mound counts in unburned grids than in burned grids (Figure 2.4). For disturbance level, expected RIFA mound count increased 75% [ $e^{\beta} = 1.75, (0.975, 2.89)$ ] in moderately disturbed areas over the expected counts in low disturbance areas. Based on the results of this analysis, I wanted to investigate if soil variables explained the influence of region.

Therefore, my second set of analyses explored the relationship of with soil variables with RIFA mound counts, specifically the percentage of sand, percentage of clay, pH, and bulk density (Table 2.3). For every 1 unit increase in pH at 15 - 25 cm, the expected number of RIFA

mounds decreased by 51% [ $e^{\beta} = 0.513$ , (0.264, 0.996; Figure 2.7). However, RIFA mound counts were not related to percentage of sand, percentage of clay, or bulk density (Appendix 3).

## DISCUSSION

The number of RIFA mounds was related to both year and region, as well as the interactions of year with burn interval and year with canopy cover. While year, region, and canopy closure were not included in my hypotheses, the hypothesis that mound counts would be related to burn interval did receive support. Evaluating the interaction of year and burn interval revealed conflicting trends. In 2016, higher RIFA mound abundance was found in unburned plots, but in 2017 higher RIFA mound abundance was found in burned plots. These conflicting trends could be a results in climatic differences between years, as 2016 had a drought during the survey period (GEPD 2016). Drought could have influenced the intensity and effectiveness of burns during individual years. Excluding burn interval effects, the variable of year was likely influenced by my level of experience, as mound detectability was higher in 2017 than 2016 (Appendix Table 1.1).

Past research has examined the independent impact of prescribed burns and other disturbance-mediated management (e.g., disking) and found little influence on RIFA presence (Forbes et al. 2002). However, my measures of burn interval and disturbance level, which includes the effect of disking, both had significant effects on the expected RIFA mound number in my study. The significance of burn intervals on properties could be a result of 2016 being a drought year, as mentioned before. The significance of disturbance level could be from higher percentages of disking than what was tested in past studies. However, the variable of disturbance level also included percentage of agricultural land use, and it has not yet been tested if agricultural land use or disking has a stronger impact on RIFA.

My hypothesis regarding soil was not supported, as RIFA mound abundance was not influenced by any of the soil variables measured. This lack of a relationship is intriguing, as there is a debate in the literature on the impacts of soil characteristics on RIFA abundance (Ali et al. 1986, Porter et al. 1991, Wangberg et al. 1980). Soil was the major factor thought to differentiate the Albany and Tallahassee regions, but results do not seem to support this hypothesis. However, it is worth noting that my range of soils did not contain much variety in percentage of clay or sand. For example, none of the surveyed properties contained areas classified as sand hills, which can be found in longleaf pine in Georgia and Florida and support gopher tortoise and eastern indigo snake populations (Stevenson et al. 2003). There were also no properties with heavy amounts of clay. Surveying a wider range in soil particle size and bulk density could alter my results.

My prediction regarding ground cover was also not supported. Properties with old field (historically agricultural) groundcover were expected to have a higher RIFA mounds abundance, as old field properties typically have higher numbers of invasive species (Keeley 2005). However, groundcover did not demonstrate a significant influence. While the lack of groundcover influence could imply that RIFA are an invasive adept at colonizing in both old field and native groundcovers, several factors may contribute to groundcover's low influence. First, all sites were regularly burned with no long-term, unburned properties available to compare RIFA abundance. Second, there were differences in both the age and management of native groundcover properties. For example, property RH4 has been maintained consistently as a virgin longleaf pine tract for ~50 years. RH5 was comparable in age, but had a disruption in burn interval when the property owner changed (Terhune, personal communication). The RH5 burn interval was restored several years ago, but the impacts of an extended unburned period could be

significant. Also, some properties that were considered native groundcover in the Albany region had randomly selected plots where hardwoods and other brush encroached on the longleaf pine and seasonal grasses. Future work could include measurements of basal area and hardwood presence within plots to determine the influence of these variables.

There was also variability in expected RIFA abundance among properties with similar groundcover (Table 2.5). For example, property RH4 had native groundcover and only 1 of 6 plots had RIFA present. In contrast, nearby property RH5 had native groundcover and 5 of 6 plots had RIFA present. The difference between these two native ground properties could be due to inconsistency in land management. Property RH5 had a period of years where prescribed burns were conducted sporadically due to changes in property ownership. While RH5 burned on a regular schedule during my study, the high number of RIFA mounds could be due to this lapse in burn regimes.

Region did influence RIFA mound numbers, but what is driving this impact can be difficult to characterize. Differences in climate and property management may contribute. Climate varied between regions, so including measures of temperature or drought (e.g., Keetch-Byram Drought Index) in future analyses could better explain the influence of region. Property management also varies by region. Specifically, properties in the Albany region typically had smaller patches of landscape due to timber harvesting practices (Terhune, personal communication). Future research could include specific percentages of disking and other land use, as well as patch size, to understand if this explains regional effect. Surveying areas with greater diversity in disturbance and soil characteristics would also refine our understanding of the variables influencing RIFA. Identifying these variables could not only aid land managers



considering control efforts for RIFA, but could also be influencing other invasive invertebrates and help us isolate invasion pathways.

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## TABLES AND FIGURES

Figure 2.1. My two study regions (Albany and Tallahassee) with stars representing the 11 properties surveyed.

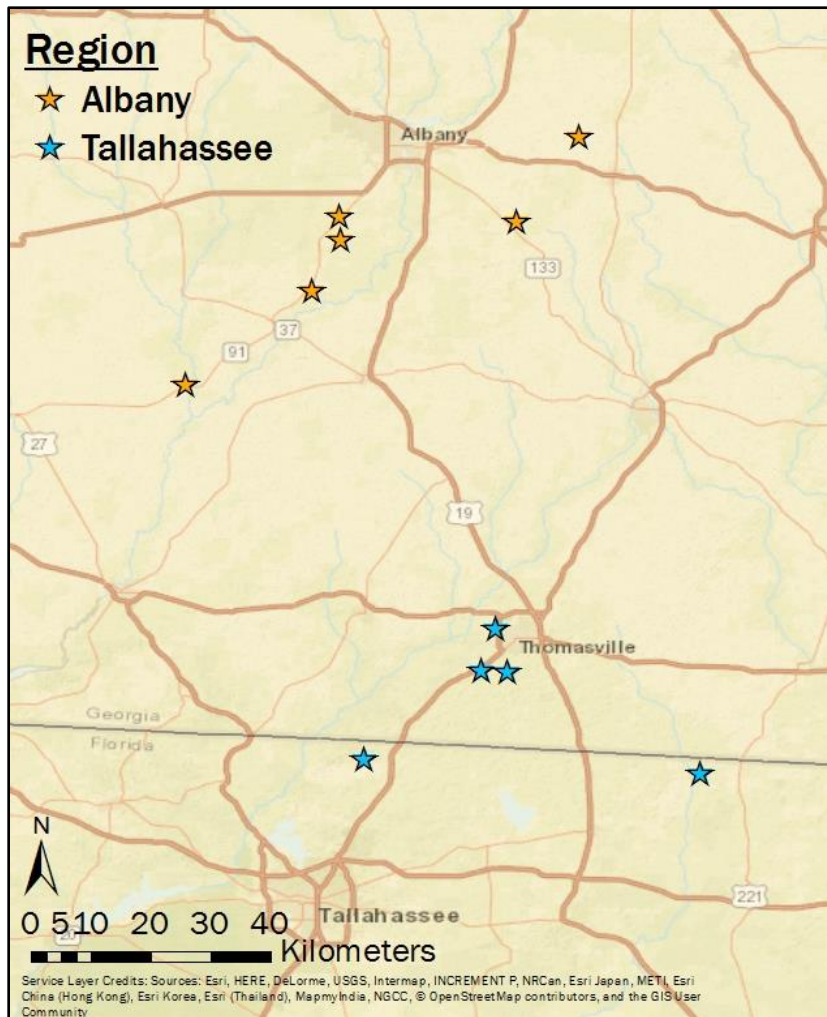


Figure 2.2. Tall Timber Research Station and the distribution of randomized plots within the property (represented by squares colored by burn interval).

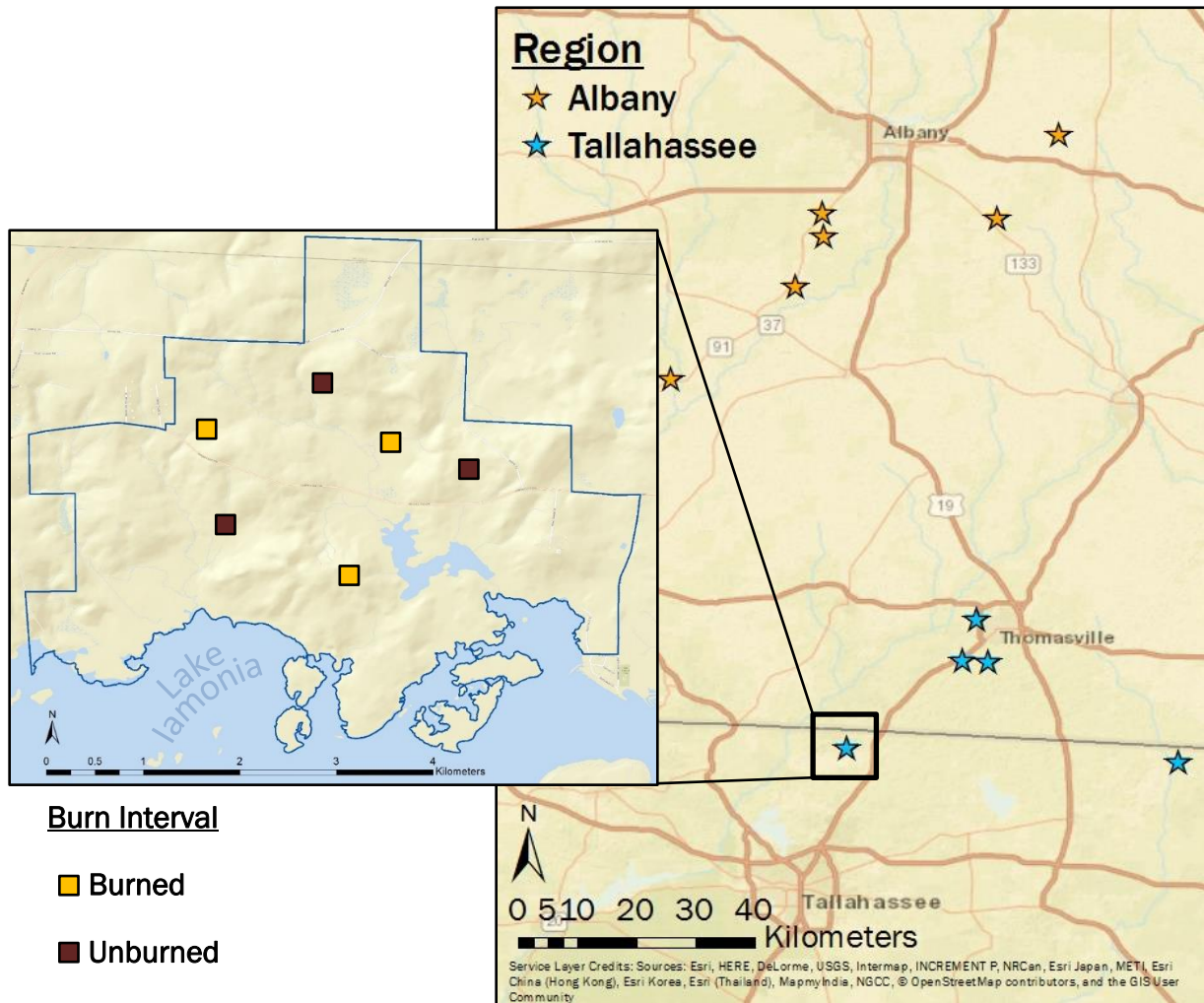




Figure 2.3. A plot with six 50 m line transects running north to south, each spaced 10 m apart. RIFA mounds within 5 m of line transect were recorded.

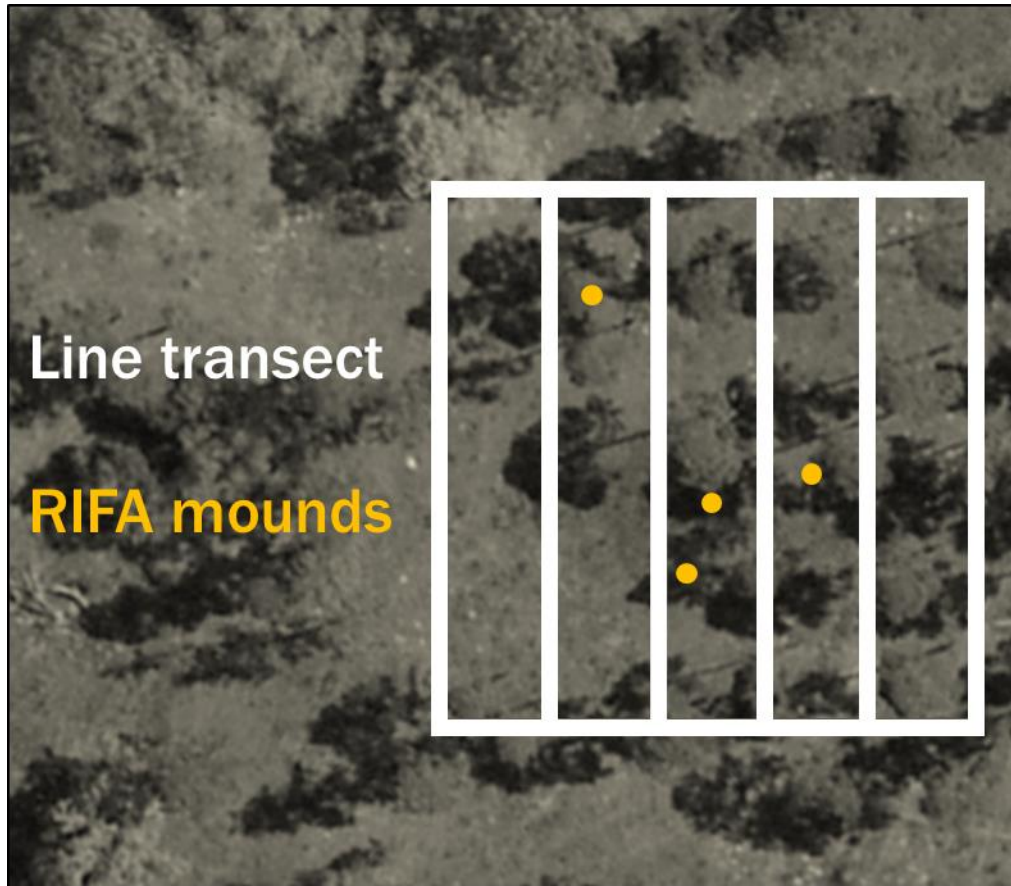
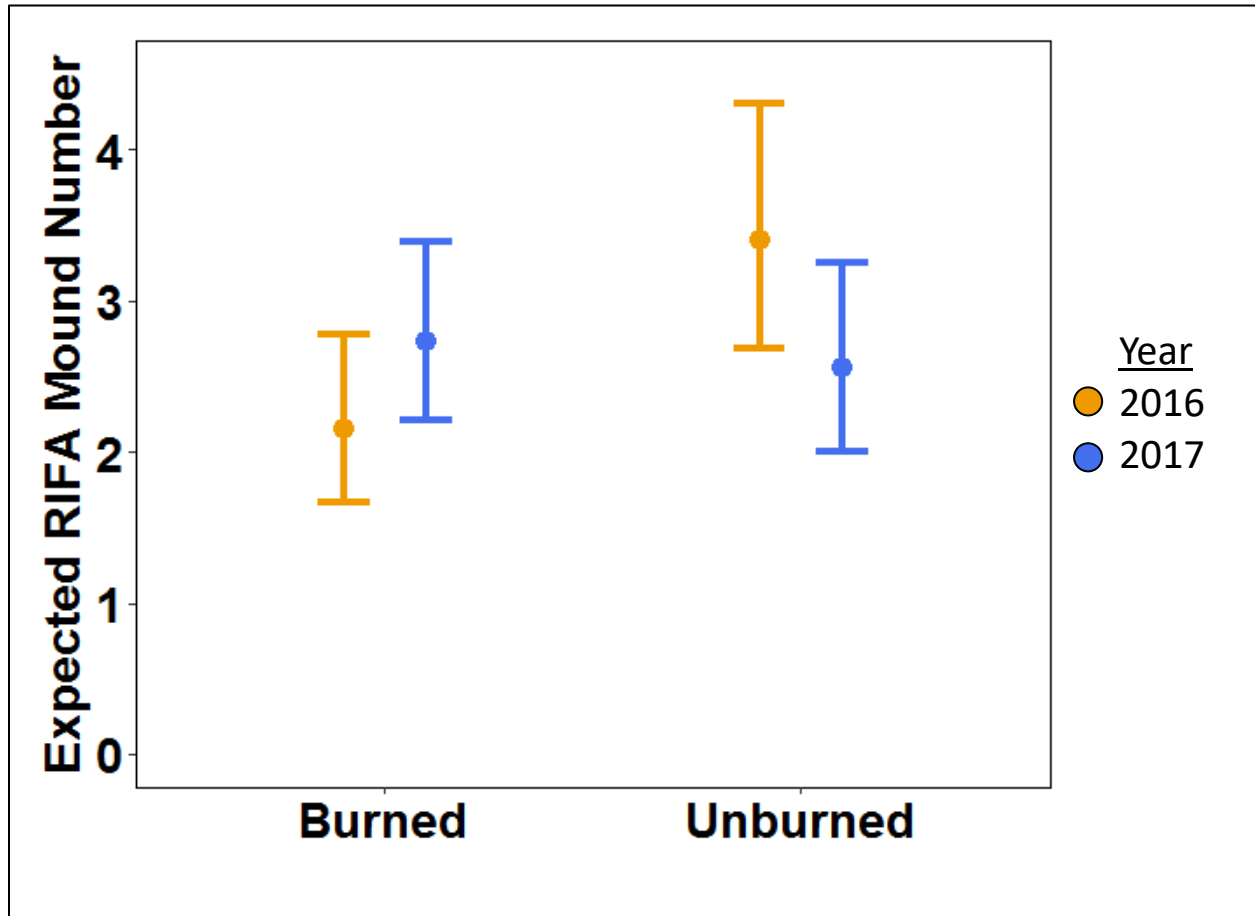
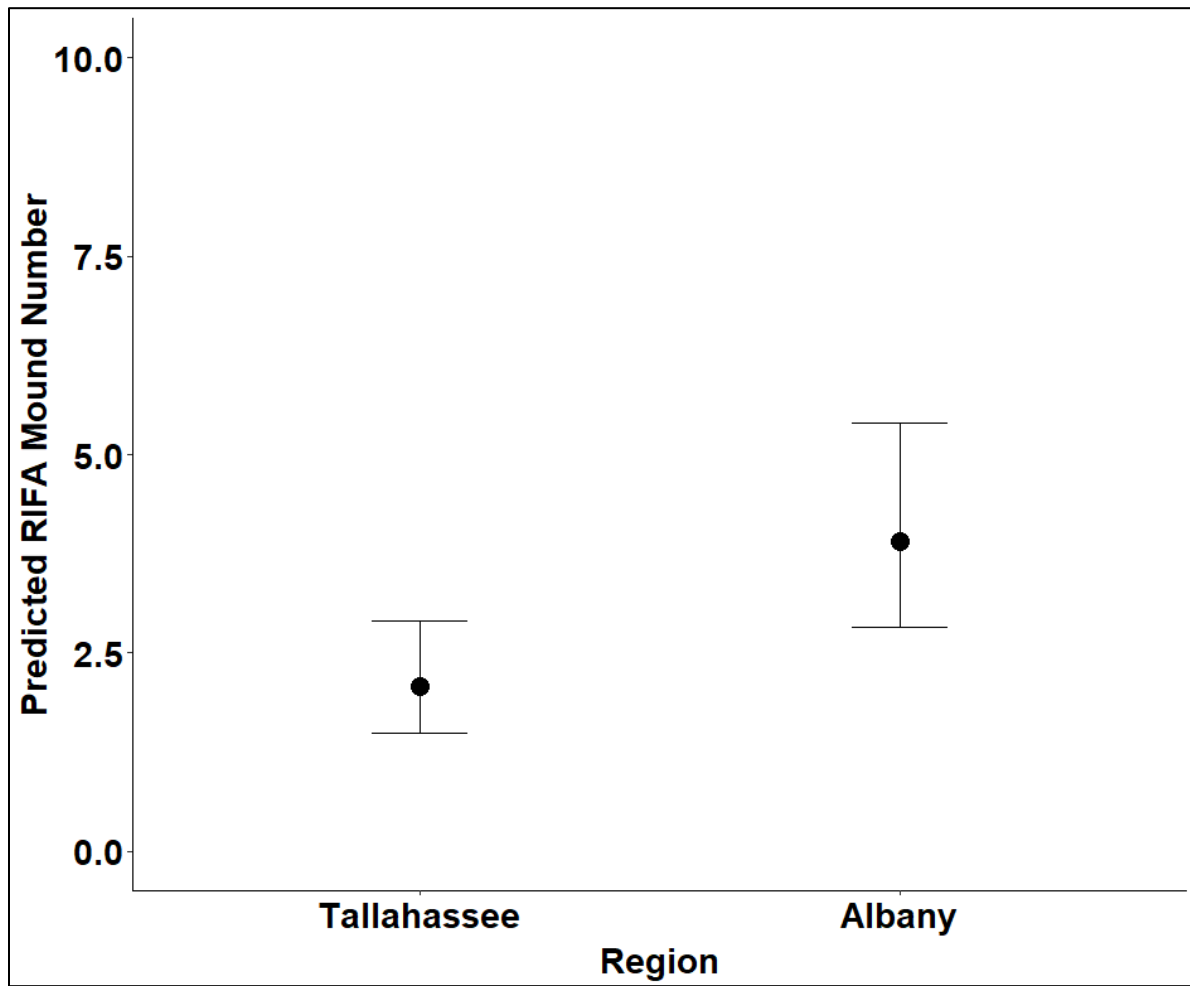


Figure 2.4. The influence of burn interval on expected RIFA mound number varied between the two study years. In 2016, unburned plots had higher expected RIFA mound numbers, but in 2017 burned plots had higher expected RIFA mound numbers.<sup>1</sup>



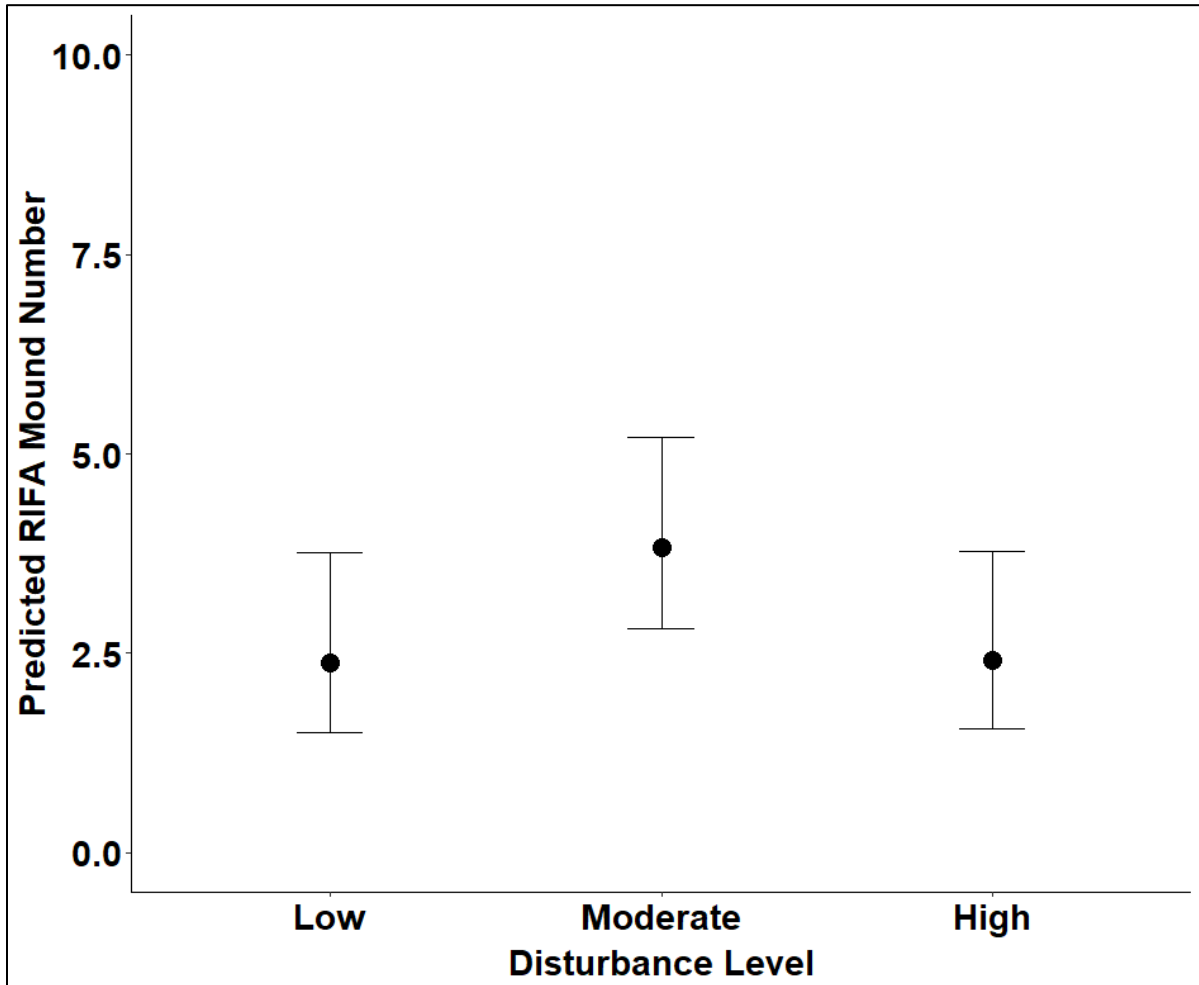
<sup>1</sup>Error bars represent 95% confidence limits.

Figure 2.5. Expected RIFA mound number was higher in the Albany region when compared to the Tallahassee region.<sup>1</sup>



<sup>1</sup>Error bars represent 95% confidence limits.

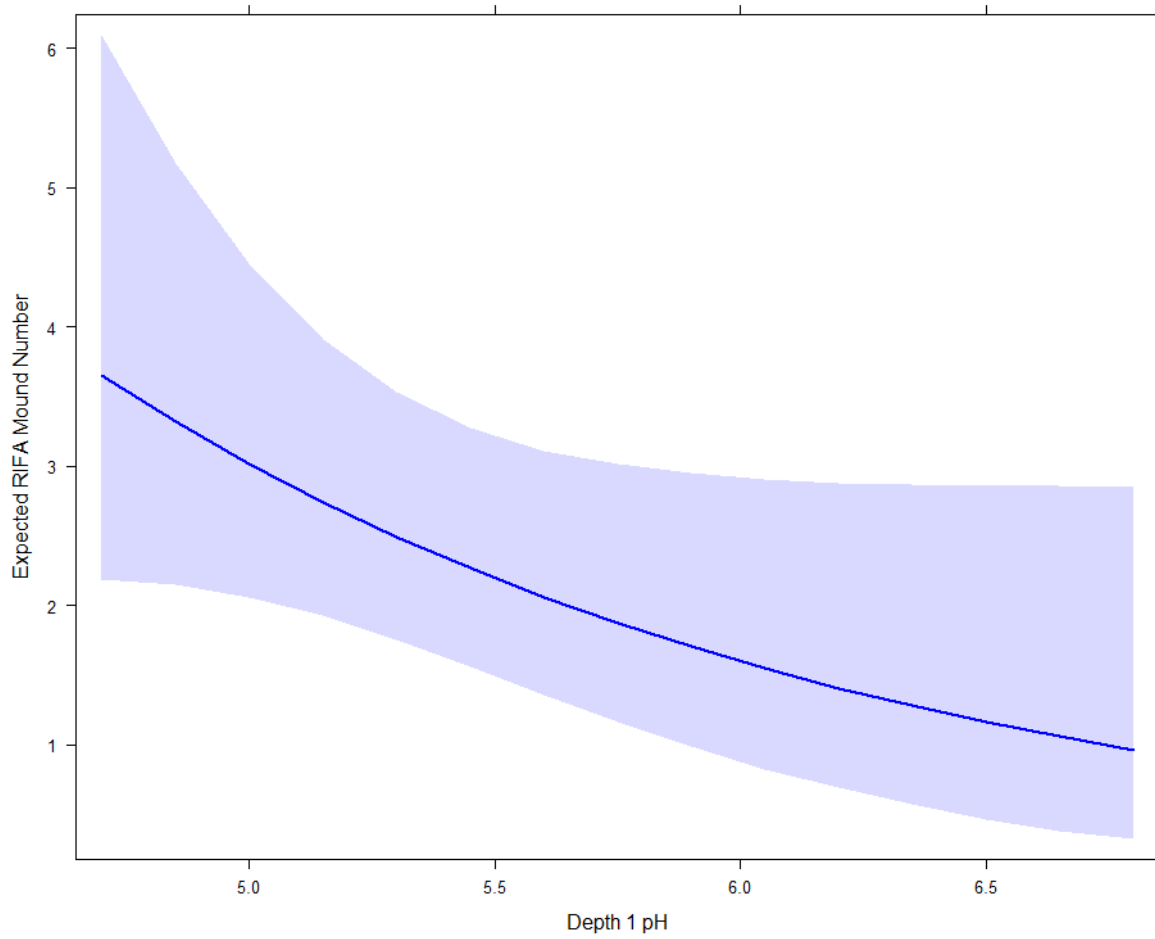
Figure 2.6. Expected RIFA mound number was higher in plots with moderate disturbance level, but there was large overlap of confidence intervals.<sup>1,2</sup>



<sup>1</sup>Low: Little to no disking or agriculture (mostly native ground properties); Moderate: Moderate percentage of land disked or used for agriculture; High: High percentage of land disked or used for agriculture.

<sup>2</sup>Error bars represent 95% confidence limits.

Figure 2.7. As the pH of soil increased, the expected RIFA mound number decreased.<sup>1</sup>



<sup>1</sup>Light blue polygon represents 95% confidence limits.

Table 2.1. Abbreviations and characteristics for the properties surveyed in my study regions of Albany and Tallahassee during 2016 and 2017.

Year	Region	Property <sup>1</sup>	Groundcover <sup>2</sup>	Burned <sup>3</sup>	Unburned <sup>4</sup>	
2016	Albany	ALB 1	OF	3	3	
		ALB 2	OF	3	3	
		ALB 3	OF	3	3	
	Tallahassee	RH 1	OF	3	3	
		RH 2	OF and NG	6	6	
		RH 3	OF and NG	6	6	
		RH 4	NG	6	0	
		RH 5	NG	3	3	
	2017	Albany	ALB 1	OF	3	3
			ALB 2	OF	3	3
ALB 3			OF	3	3	
ALB 4			NG	3	3	
ALB 5			NG	3	3	
ALB 6			NG	3	3	
Tallahassee		RH 1	OF	3	3	
		RH 2	OF and NG	6	6	
		RH 3	OF and NG	6	6	
		RH 4	NG	6	0	
	RH 5	NG	3	3		

<sup>1</sup> ALB= Albany region; RH= Tallahassee region

<sup>2</sup> OF= Oldfield groundcover; NG= Native groundcover

<sup>3</sup> Number of burned plots

<sup>4</sup> Number of unburned plots

Table 2.2. Estimated effects and Type II likelihood ratio tests for terms included in final model for red imported fire ant mound counts at 78 sample grids in Florida and Georgia.

Parameter	$\beta$	S.E. <sup>2</sup>	95% Confidence Limits	LRT Statistic <sup>4</sup>	P
Year	0.546	0.401	-0.014, 1.11	0.238	0.631
Groundcover	0.006	0.229	-0.451, 0.477	0.001	0.525
Burn Interval	0.485	0.199	0.097, 0.880	2.64	0.052
Canopy Closure	0.167	0.509	-0.843, 1.16	0.390	0.435
Region	-0.826	0.269	-1.37, -0.291	9.44	0.002*
Disturbance level (Moderate)	0.558	0.250	-0.026, 1.06	7.98	0.019*
Disturbance level (High)	0.044	0.391	-0.803, 0.826	7.98	0.019*
Interaction of year and burn interval	-0.592	0.317	-1.23, 0.033	3.48	0.062
Interaction of year and canopy closure	-0.717	0.476	-1.65, -0.215	2.15	0.132

<sup>1</sup>Random effects= Property (variance=0.000, standard deviation=0.000),

Grid (variance=0.300, standard deviation =0.548)

<sup>2</sup> All degrees of freedom = 1, with the exception of Disturbance level (degrees of freedom = 2)

<sup>3</sup> Standard error

<sup>4</sup>Likelihood ratio test statistic

\*Statistically significant



Table 2.3. How the percentage of RIFA mounds observed on a survey property would compare to the baseline estimate.

Region	Property <sup>1</sup>	Groundcover <sup>2</sup>	Property Effect
Albany	ALB 1	OF	0.967
	ALB 2	OF	0.892
	ALB 3	OF	0.929
	ALB 4	NG	0.998
	ALB 5	NG	1.11
	ALB 6	NG	1.29
Tallahassee	RH 1	OF	1.12
	RH 2	OF and NG	1.25
	RH 3	OF and NG	0.898
	RH 4	NG	0.771
	RH 5	NG	1.19

<sup>1</sup> ALB= Albany region; RH= Tallahassee region

<sup>2</sup> OF= Oldfield groundcover; NG= Native groundcover

**Chapter 3: Falling for fire ants: Assessing fire ant prevalence in burn-mediated ecosystems  
and their impacts on native ant populations.**

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## *Abstract*

Invasive invertebrates are often a subject of study due to their impacts on human and ecosystem health, but their impacts on local invertebrates are less known. Using the red imported fire ant (RIFA, *Solenopsis invicta*) as a model species, I investigated how RIFA or other environmental variables, such as habitat disturbance, influenced native and non-native ant biodiversity.

Specifically, I hypothesized that as RIFA mound and forager abundance (i.e. level of activity) increased, there would be a decrease in native and increase in non-native ant species richness. To test my hypothesis, I sampled ants on 11 properties in Florida and Georgia managed with frequent fire. Variables affecting ant biodiversity were analyzed with Poisson models and Akaike's information criterion. Results indicate that as the number of RIFA increase, there is a decrease in native and increase in non-native ant species richness. This implies that RIFA may be impacting ecosystem services from native ants and are not displacing non-native ants.

Key words: ant biodiversity, pine savannah, pitfall trapping, red imported fire ants

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Invasive species are one of the biggest threats to biodiversity in our time (Bellard et al. 2016, Clavero et al. 2009, MEA 2005). Biological invaders increase animal extinctions (Clavero and García-Berthou 2005), compete with native species for resources (Wojcik et al. 2001), and impair ecosystem services (Pejchar and Mooney 2009, Pyšek and Richardson 2010). However, the severity of impact from invasive species varies across region and taxa (Bellard et al. 2016), making it difficult for conservation efforts to determine where and when management is necessary, as high costs of invasive control are an additional draw on the limited resources available for conservation efforts.

Research on invasive species has been prolific in the recent decades, but gaps still remain in our knowledge of how invasion can impact local species assemblages and the ecosystem services they provide. Invertebrate invaders are a serious threat around the world to the health of both humans and ecosystems, but research involving invasive invertebrates commonly focuses on their impact on vertebrate or plant species (Green and O'Dowd 2009). For example, invasive mosquitoes are frequently studied for their potential of transmitting disease to vertebrates (Juliano and Lounibos 2005), while other invertebrates such as invasive wasps and moths are studied for negative impacts on plant species (Beggs 2001, Lovett et al. 2006). The approximately 1.1 million known arthropods (predominantly insects) make up half of the described species on Earth (Hawksworth and Kalin-Arroyo 1995, Hamilton et al. 2010), but large-scale invertebrate monitoring is uncommon and therefore the influence of invasive invertebrates on their native equivalents is poorly understood. Native invertebrates provide important ecosystem services such as seed dispersal (Heithaus 1981, Kalisz et al. 1999), decomposition (Lavelle et al. 2006), and soil aeration (Stork and Eggleton 1992). If these native invertebrates are displaced by invasive invertebrates, it is possible that ecosystem services will

be lost (Stubble et al. 2005). The potential loss of ecosystem services, as well as potential loss of biodiversity, warrants more research into relationships of competing invasive and native invertebrates.

Red imported fire ants (*Solenopsis invicta*; hereafter, RIFA) provide a model taxon for examining the relationships between invasive and native invertebrates. RIFA have historically been linked to decreased native ant diversity, primarily through competition (Tschinkel 1988, Porter and Savignano 1990, Plowes et al. 2007). However, the mechanisms underlying the impacts on native ant communities remains uncertain (Hill et al. 2013). Current research suggests that RIFA may weakly influence native ant communities through superior competition for resources, while soil disturbance or disruption in native vegetation from disturbance regimes, such as prescribed burning, have greater impacts (King and Tschinkel 2006 and 2013a). However, there is no consensus on this topic (Stubble et al. 2013, King and Tschinkel 2013b), indicating that more research is needed.

The majority of past research investigating RIFA impacts on native ants has been done in small scale studies. Using a larger scale may reveal relationships that are harder to define at a small scale and allow use of greater environmental gradients. Also, while there has been research investigating the effect of prescribed burning has on RIFA abundance and native ants (Forbes 2002), scant information exists on what environmental variables interact with prescribed burning and its frequency. High variability in RIFA depredation on ground-nesting birds between landscapes managed with prescribed burning (Haines et al. 2017) suggest that other variables, such as soil properties or site disturbance history (Keeley 2005), influence colonization and persistence of RIFAs.

Therefore, similar variation may exist in RIFA numbers and local ant community

assemblage. I hypothesize that RIFA abundance will impact the forager abundance of native and non-native ant species. Specifically, I predict that as RIFA mounds and foragers increase, there will be a decrease in native and increase in non-native ant foragers. My study will shed light on the role of RIFAs in biodiversity loss, and if native ant assemblages are negatively impacted the results will inform management and conservation efforts for native ants and the ecosystem services they provide.

## METHODS

### *Study Area*

My study was conducted on 11 private properties in southwest Georgia and north Florida (Figure 3.1), which is a large ecoregion compared to past research (Figure 3.1). On each property, 6 plots were randomly sampled for ant using a randomized block design (Figure 3.2). Each study site occurred in one of two regions: Albany and Tallahassee. Albany study sites were located in Baker and Dougherty counties, Georgia, and the other in Leon and Jefferson counties, Florida. In the Albany region, I surveyed three hunting properties with old-field groundcover, embedded in a 120,000 ha landscape of similar properties. These properties consist of low basal area (9.2–13.8 m<sup>2</sup> per ha), old field pine forests in an open pine-grassland structure maintained through commercial thinning and prescribed fire, with small fallow fields throughout the area (Palmer et al. 2012). Predominant timber among uplands includes longleaf pine and slash pine (*P. elliotii*), with scattered hardwoods such as live oak (*Quercus virginia*), southern red oak (*Q. falcata*), and water oak (*Q. nigra*). Herbaceous cover is predominantly warm season grasses, such as broomsedge (*Andropogon* sp.), annual broad-leaved forbs, and legumes (Burger et al. 1998). Old-field habitats are designated by land-use change such that they were converted to agricultural fields, in the 1800s, followed by agricultural abandonment, in the 1900s, and seeded

back to pine and native vegetation maintained by prescribed fire. I also sampled three properties with native groundcover (predominately mature longleaf pine and wiregrass (*Aristida stricta*)) individual, specifically in the Dougherty and Worth counties.

The average growing season for the Albany region during this study was mid-March to the end of November, with an average temperature of 24.4° C (NOAA, Weather Underground). The average annual precipitation for Albany was 127 cm, with an average of about 69 cm during the May-August field season (NOAA, Weather Underground). Topography on all Albany properties is relatively flat with few to no hardwood drains.

In the Tallahassee Region, I surveyed three properties in the Leon and Jefferson counties near Tallahassee, Florida. The two old field properties in Leon county are embedded in an approximately 161,874 ha landscape of bobwhite management properties. The property in Jefferson County is approximately 3,682 ha surrounded by properties of similar land management. All three old field properties consist of old field pine forests, mostly loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), interspersed with hardwood drains, hammocks, and small fallow fields. Pine forests are maintained for an open pine-grassland structure through prescribed fire. Herbaceous groundcover is a mix of warm season grasses, legumes, and forbs (Hammond 2001). Also in the Tallahassee region are four properties with native groundcover (predominately mature longleaf pine and wiregrass), specifically in Thomas county, Georgia, and Jefferson county, Florida.

The average growing season for the Tallahassee region was mid-March 15 to the end of October. The counties around Tallahassee had an average temperature of 25.6° C and an average annual precipitation of 158 cm, with an average of about 66 cm during the May-August field season (NOAA, Weather Underground).

Properties in both regions are similarly managed with prescribed fire, typically occurring in March and April of each year. Old field properties burn on a rotation, with managers burning ~50-70% of the property and then burning the unburned area the following year (Palmer et al. 2012). Properties with native groundcover varied, most being burned on a similar rotation to the old field properties. However, two native groundcover properties are burned completely each year (properties RH4 and RH5, see Table 3.1).

Soils on the Albany properties are classified as Orangeburg-Lucy-Grady and Norfolk-Wagram-Grady soil associations, which are predominantly sandy-loam textured soils with moderate permeability and low natural fertility (Palmer et al. 2012). Soils in the Tallahassee region are of the Fuquay-Orangeburg-Faceville soil association, characterized by well drained, moderately fertile fine-loam soils with varying amounts of sand and clay (Palmer et al. 2012). The Orangeburg series is common in both the Albany and Tallahassee regions, but otherwise there are no shared soil families, meaning soils between regions vary in characteristics like horizonation, mineral composition, and permeability.

#### *Ant Surveys*

On each of six properties in the Albany region and five properties in the Tallahassee Region, I randomly sampled six plots ( $50 \times 50$  m each, Figure 2.2) with six transects each (Figure 2.3, Table 2.1). Of the 11 total properties, 8 were sampled in 2016 and 3 were added in 2017 (plots: 2016  $n = 60$ , 2017  $n = 78$ ). In areas with two burn types, I surveyed three burned and three unburned plots per property (2016: burned  $n = 36$ , unburned  $n = 24$ ; 2017: burned  $n = 44$ , unburned  $n = 34$ ). Burned plots had been burned during March or April of the survey year, while unburned plots were last burned March or April of the previous year. Because I sampled for two consecutive years, most of the initially burned plots in 2016 became unburned plots in



2017. To choose study plots, I generated 100 random points on property shapefiles in ArcGIS (ESRI 2016), then selected the first three points in burned and unburned areas that were 50 m from known roadways. Old field properties (~9 ha) have annual burns in the spring on a rotating schedule, allowing both burned and unburned areas to be sampled. The native ground properties (~10.5 ha) serve as an example of less disturbed landscapes, as they have minimal sources of disturbance beyond prescribed fire.

Data were collected from May-August for all properties, with eight sites surveyed in both years and three only surveyed in 2017. I systematically sampled each plot using 6, 50 m transects per plot (Forbes et al. 2000), 10 m apart and oriented north to south (Figure 3.3). While randomly placed, the edges of plots were all roughly 50 m away from any road-ways to reduce disturbance associated with roads (Forbes et al. 2000).

To quantify RIFA mound numbers, an observer walked transects inside a plot and searched for mounds that were within 5 m of each transect. When located, a mound was tested for occupancy by probing the top several times with a trekking pole. If ants swarmed, they were examined to determine species. Mounds of RIFA were marked as active, measurements were taken for mound dimensions and perpendicular distance (m) from transect, and GPS coordinates were gathered using a Trimble GEO Explorer 7x unit with 1 - 100 cm accuracy. GPS coordinates for the corners of plots were also recorded so that surveys could be repeated in the same areas (on a different burn interval) in both years. The mound dimensions were also measured and recorded to the nearest cm.

To identify local ant assemblages, I deployed pitfall trap transects 25 m north and south of the mound survey plots (Figure 3.3). Both pitfall transects were 50 m long, with six Norlander pitfall traps placed 10 m apart (2016: n = 576, 2017: n = 792; see Figure 3.4). To reduce lab

processing of 2017 samples, ants were identified from even numbered traps from each line of pitfall traps (n = 396) for all properties. In pitfall analysis, ants were isolated from trap contents and then identified to species using the southeastern ant identification key created by MacGowan (2018).

### *Environmental Variables*

During 2017, I evaluated canopy closure from the center of the plot were determined with a canopy densitometer. Property disturbance level was also categorized into low, moderate, and high levels. These levels were characterized by percentage of disking and agricultural land use according to management records and satellite data.

### *Data Analysis*

In 2016, 23,799 total ant foragers were collected (burned n = 12,403, unburned n = 11,396), and in the following year 10,580 total ant foragers were collected (burned n = 6,620, unburned n = 3,960) from my subset of pitfalls. Of these ants, I collected 64 native species and 11 non-native species (excluding RIFA, Appendix Table 4.1). All analyses were performed in R (R Core Team 2018, Appendix 2). Based on low occurrence of zero counts in my data set and low overdispersion (overdispersion = 1.15 for full model), I used Poisson models with trap effort per plot  $\times$  year as an offset. I outlined the *a priori* hypotheses about the eight variables incorporated in my model suites (Table 3.2).

Sequential model fitting was used to evaluate the relative importance of covariates based on my candidate hypotheses in each modeling step (Dinsmore et al. 2002, Conkling et al. 2015). Each model set was composed of explicit candidate hypotheses established *a priori* where the best fitting model was used as the baseline model in the next model set to evaluate additional hypotheses relative to explicit variables related to ant assemblages. I first fit a set of models

(Suite 1) examining large-scale effects (region and year) on my response variables. The second model set included the best model from Suite 1 as a baseline model, with Suite 2 models formed by adding alternative combinations of other covariates based on a priori hypotheses. I applied this sequential modeling approach into two separate sets of analyses for each of the two primary response variables: total observed native richness in a plot  $\times$  year sample, and total observed non-native richness (excluding RIFA, code in Appendix 2).

Using an information-theoretic approach, I compared candidate models by employing Akaike's Information Criterion (AIC) such that the model with the lowest AIC value was considered the best approximating model (Akaike 1973, Burnham and Anderson 1998, Johnson and Omland 2004, Anderson et al. 2000). I further assessed the relative plausibility of each model using Akaike model weights ( $w_i$ , Anderson et al. 2000, Burnham and Anderson 2002), where the model with the higher weight value was the best approximating model. As such, I report proportional effects by exponentiating beta estimates and respective 95% confidence intervals for variables in my top models (e.g., season, precipitation, temperature) to provide additional inference on their biological importance to survival (Nakagawa and Cuthill 2007). To further compare and isolate individual parameter effects, I summed model weights while keeping the number of candidate models similar for all parameters of interest (Terhune et al. 2007).

## RESULTS

The top three models indicated a relationship between RIFA mound number and native ant species richness (Table 3.4). The interaction of RIFA mounds and region had the largest impact on native ants (Table 3.5). In the Albany region, as RIFA mound counts increased by 1, the expected native ant species richness decreased by 5% [ $e^\beta = 0.950$  (0.919, 0.983)]. In the Red Hills region, as RIFA mound counts increased by 1, the expected native ant richness decreased

by 2% [ $e^\beta = 0.982$  (0.956, 1.01)]. Ignoring interactions, the overall expected native ant species richness was 53% [ $e^\beta = 1.53$ , (0.991, 2.39)] higher in the Red Hills region than in Albany. In terms of year, the expected native ant species richness was 37% [1.37, (1.24, 1.51)] higher in 2017 than in 2016 (Table 3.6).

The second top model for native ant numbers was very similar to the first model in AICc weight, and did not include an interaction with region. In 2017, the expected native ant species richness was 36% [ $e^\beta = 1.36$ , (1.23, 1.51)] higher than in 2016. For the Albany region, overall expected native ant species richness was 43% [ $e^\beta = 1.43$ , (0.946, 2.19)] higher than expected numbers in the Tallahassee region. As RIFA mound counts increased by 1, the expected native ant species richness decreased by 3% [ $e^\beta = 0.969$  (0.949, 0.991)].

In terms of variables impacting the number of non-native ant species richness, three different variables were found in the top three models (Table 3.7). The top model included the interaction of the number of RIFA foragers and region and had a much higher AICc weight than the other two models (Table 3.8, Table 3.9). In 2017, the expected non-native ant species richness was 78% [ $e^\beta = 1.78$ , (1.44, 2.19)] higher than in 2016 (Table 3.10). In the Albany region, as RIFA forager number increased by 10% the expected non-native ant species richness increased by 0.4% [ $e^\beta = 0.969$  (0.949, 0.991)]. In the Tallahassee region, as RIFA forager number increased by 10% the expected non-native ant species richness increased by 0.3% [ $e^\beta = 0.969$  (0.949, 0.991)]. Ignoring interactions, the overall expected non-native ant species richness was 5% [ $e^\beta = 0.474$ , (0.318, 0.706)] higher in the Tallahassee region than in Albany.

## DISCUSSION

My results support the predictions that with higher RIFA numbers, there would be a decrease in native and increase in non-native ant species richness. Specifically, RIFA mounds

explained variation in native ant species richness while number of RIFA foragers explained variation in expected non-native ant species richness. Disturbance level had minimal effect on native or non-native ants. My results support arguments that RIFAs are drivers of biodiversity loss in my study sites, which agrees with some past findings (Stubble et al. 2013). Notably, disturbance level had minimal effects of ant assemblages, which differs from previous findings (King and Tschinkel 2013b). The seemingly low impact of disturbance level could be a result of partial confounding between region and disturbance level. All properties with high disturbance levels were located in the Albany region. To address this confounding relationship, further analyses will be conducted to isolate the effects of my categorical variables.

If RIFAs are impacting native ant assemblages, then it is likely that RIFAs are also impacting the ecosystem services native ants provide. The potential for RIFA impacts on ecosystem services has implications for overall ecosystem health, as native ants are important for seed dispersal and soil quality (Heithaus 1981, Zettler et al. 2001). There is currently a debate in the literature on how effective RIFAs are at fulfilling these ecosystem services if native ants are displaced. Specifically, RIFAs could increase seed dispersal (Stubble et al. 2010), but other studies have yielded increased amounts of seed destruction or dispersal in areas that are not ideal for germination (Zettler et al. 2001).

The impact of RIFAs on non-native ant species could also have implication on ecosystem services, as both may impact native ant species. However, the relationship between RIFA and non-native ant species richness could be due to a variety of reasons. For example, RIFA displacing native ants could provide more invasion opportunities for non-native ants. RIFAs and other non-native ants could also be taking advantage of similar environmental variables to colonize an area (Tschinkel 2006). These variables would be harder to identify, as variables of

disturbance level, groundcover, and burn interval did not have much impact on these two groups of ants.

Several variables related to ant biology could have influenced my overall results and warrant further analysis. For example, foraging guild may be influencing what ant species are present, as the majority of non-native ant species were predatory. It would also be helpful in future research to identify if RIFA colonies were monogynous (single queen) or polygynous (multiple queen; Porter and Savignano 1990, Helms and Vinson 2001). While polygynous colonies have not been documented in my study area, it is possible that they are present and their social behavior does influence the competitiveness of these RIFA with other ant species (Helms and Vinson 2001).

Another important variable that could be examined further is time of RIFA introduction to my study regions. Time of introduction has been a strong influence in native ant biodiversity recovering from RIFAs in past studies (Helms and Vinson 2001, Strayer et al. 2006). While several studies on RIFA have taken place in Georgia and Florida, it is difficult to find a well-documented time of RIFA introduction in my study regions. To better understand the temporal trends of RIFA invasion, future research could better isolate the impact of RIFA on native ants by using an experimental control area to exclude RIFA. Surveying an area that excludes RIFA for several years would help quantify how an ant community changes over time when not competing with RIFA.

Outside of variables related to ant biology, having wider variety in environmental variables could help future research. For example, disturbance level was a categorical variable that gave a rough estimate of disking and agricultural land use in my study regions. With more landscape data, I could use more precise estimates of disking and agricultural area which could

influence my model results. Surveying sites with more varied burn interval (e.g., one year, two years, three years, etc.) could also better isolate the influence of burning on ant communities and non-native ant success. Better quantifying environmental variables like these will be important in future control efforts of RIFA as they gradually spread northward with climate change (Gotelli and Arnett. 2002, Morrison et al. 2005).

Management decisions based off my results would need detailed cost-benefit analysis. Stakeholders that want to conserve the ecosystem services provided by native ant species by controlling RIFA would need to use precise methods to remove RIFA while not harming native ants. For example, treating a whole property for RIFA usually involved aerial dispersal of chemical agents, which can be harmful to native ant species. More targeted control of RIFA is possible, but can have high labor and monetary costs. Whether this option is worth the investment would need to be determined on a case-by-case basis.

Despite the complexity of management decisions that can come from this project, my results adds exciting information to the conversation surrounding RIFA and their impacts on biodiversity. RIFA provide an ideal model species for invasive species and can be invaluable for advancing invasion ecology, particularly as RIFA spread northward from the southeastern U.S. (Morrison et al. 2005). Identifying what environmental variables facilitate invasion by RIFA and other non-native invertebrates can help improve efforts to conserve global biodiversity.

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Zettler, J. A., T. P. Spira, and C. R. Allen. 2001. Ant–seed mutualisms: can red imported fire ants sour the relationship? *Biological Conservation* 101: 249–253.

## TABLES AND FIGURES

Figure 3.1. My two study regions (Albany and Tallahassee) with stars representing the 11 properties surveyed.

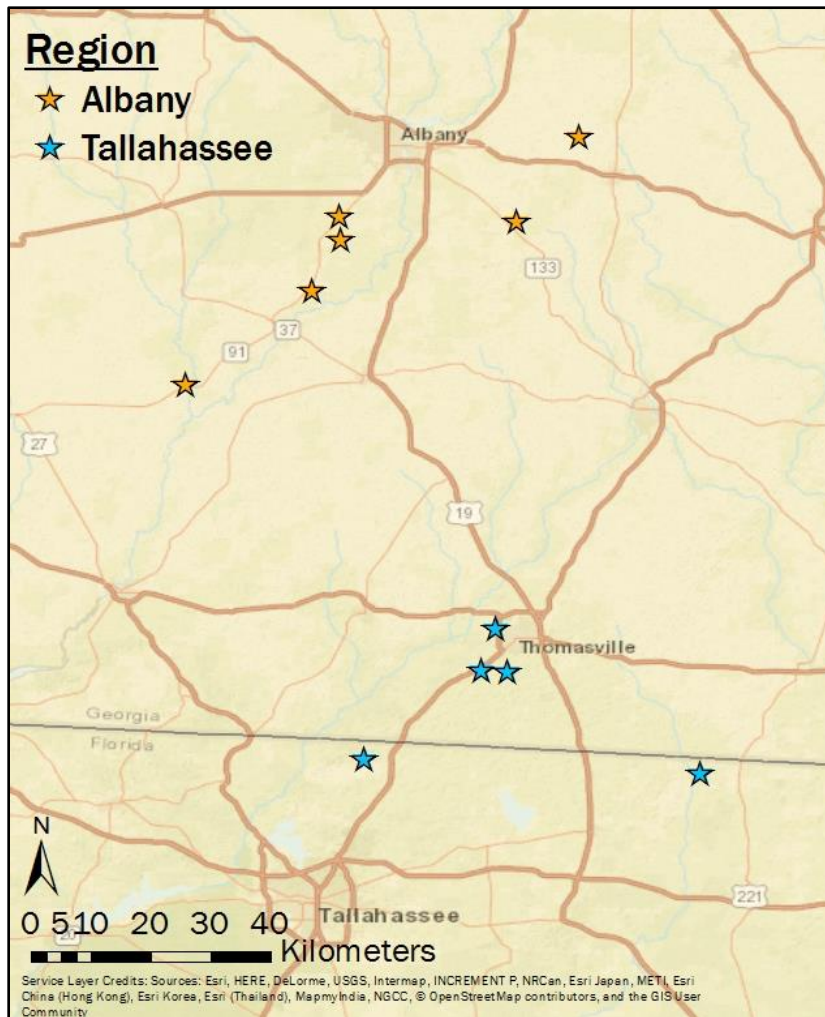


Figure 3.2. Tall Timber Research Station and the distribution of randomized plots within the property (represented by squares colored by burn interval).

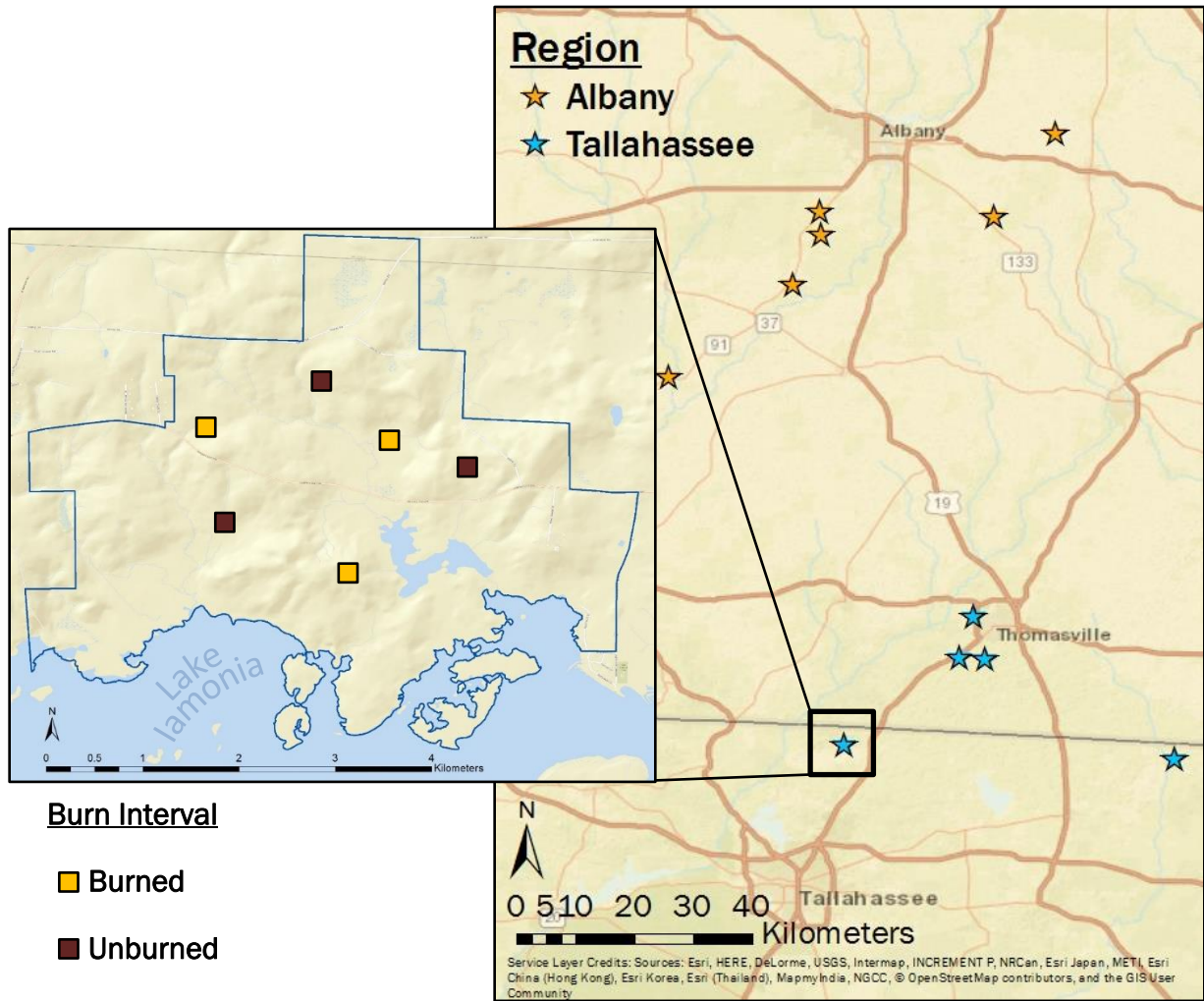




Figure 3.3. A plot with six 50 m line transects running north to south, each spaced 10 m apart. RIFA mounds within 5 m of line transect were recorded.

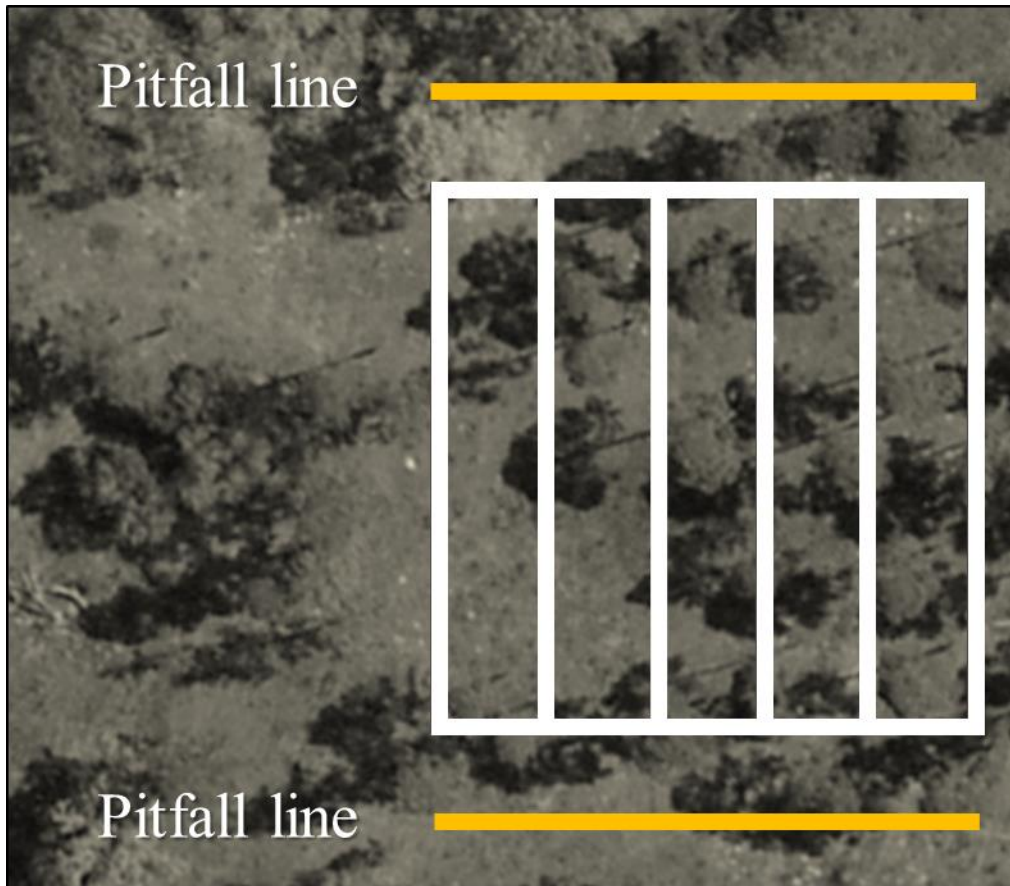
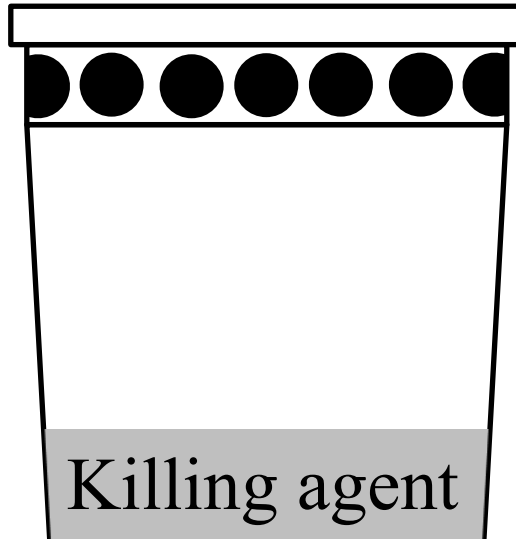


Figure 3.4. (A) The Nordlander pitfall trap design with ~24 4 cm holes drilled along the top rim of the trap to allow invertebrates to enter but exclude vertebrate species. (B) Nordlander pitfall trap deployed in the field.

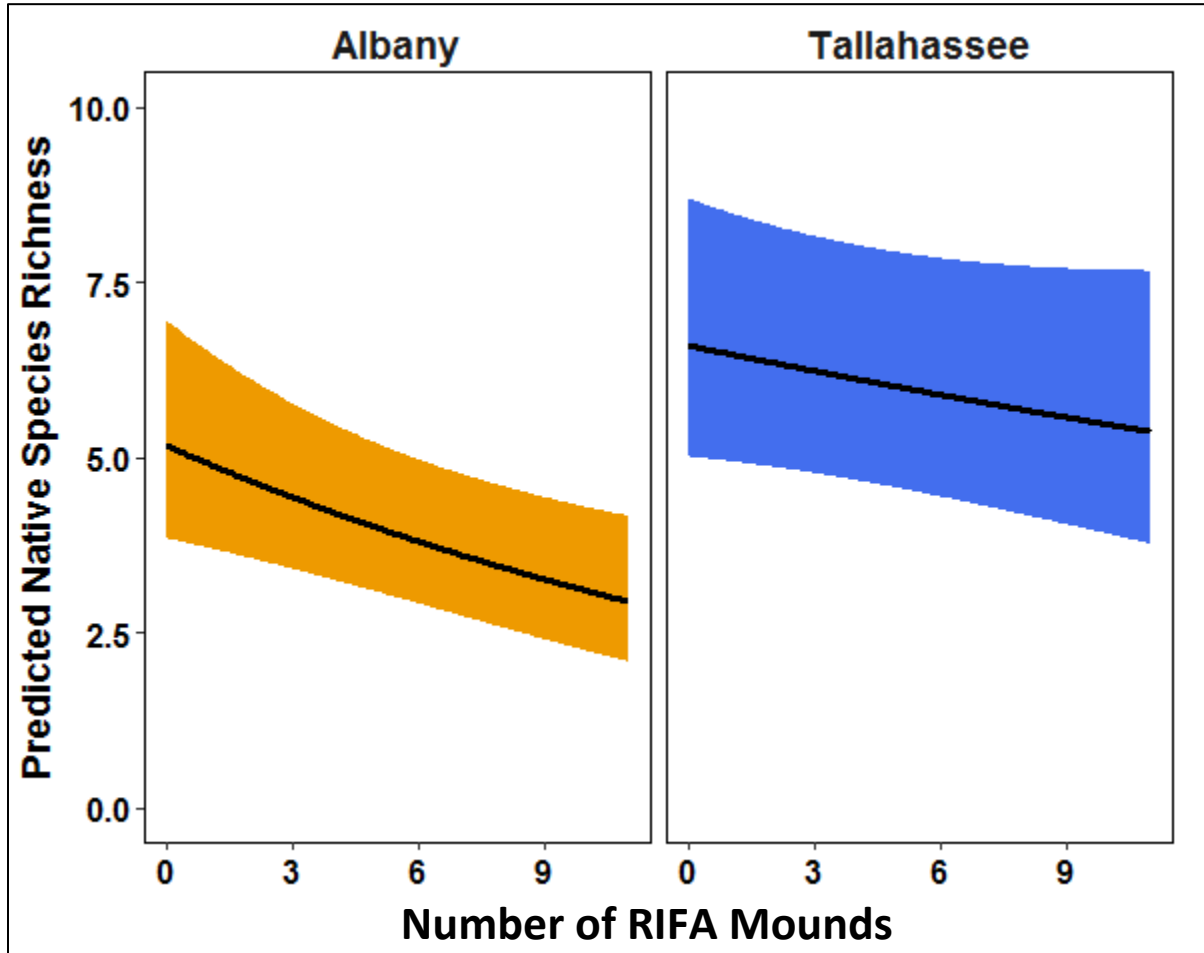
(A)



(B)

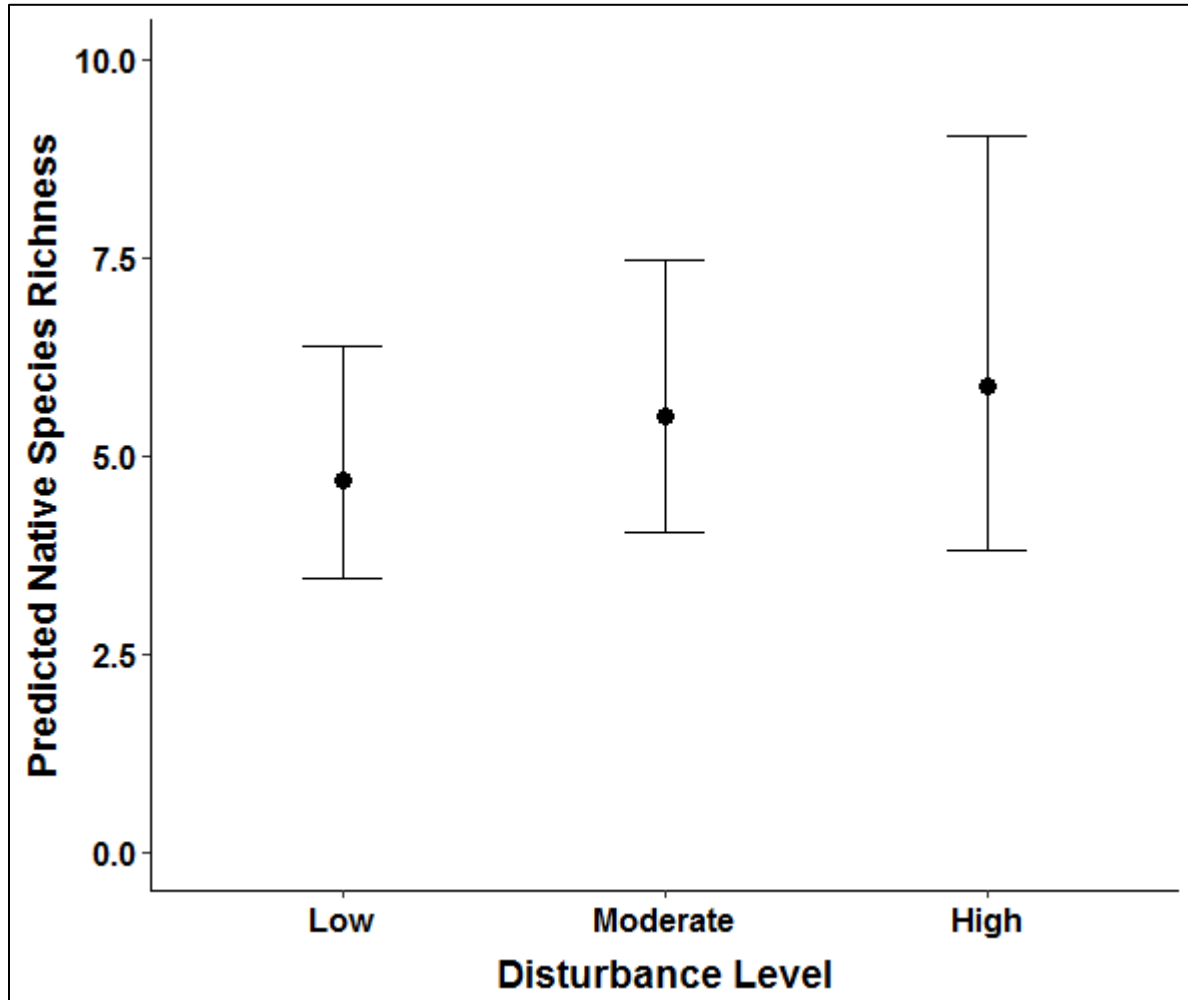


Figure 3.5. Relationship between predicted native ant species as the number of RIFA mound increase for both the Albany and Tallahassee regions. The colored sections represent the confidence limits of the data.<sup>1</sup>



<sup>1</sup>Error polygons represent 95% confidence limits.

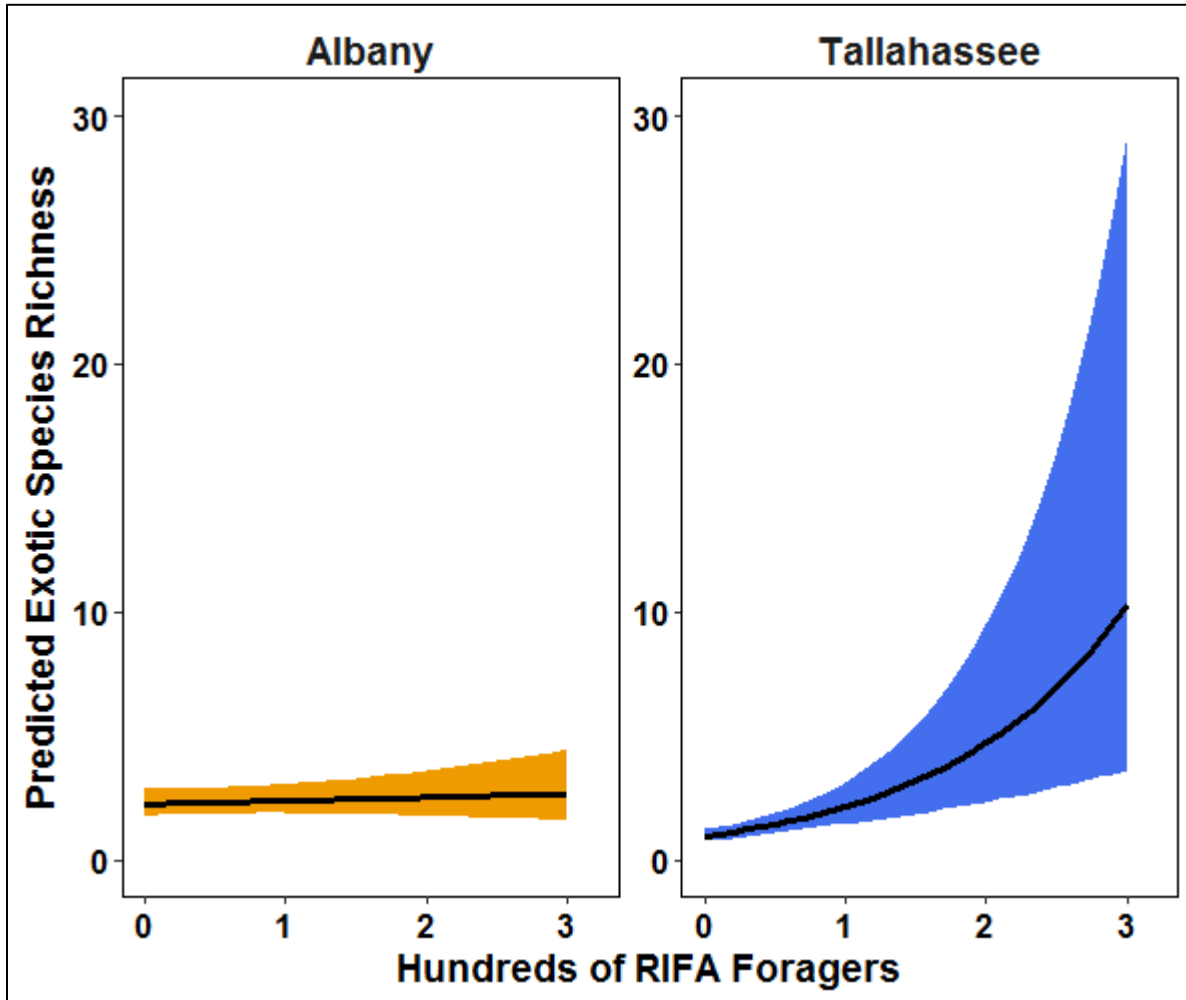
Figure 3.6. Relationship between the predicted native ant species richness and disturbance level. The lowest disturbance level includes my native groundcover areas, while the moderate and high levels include increasing percentages of property disking.<sup>1,2</sup>



<sup>1</sup>Low: Little to no disking or agriculture (mostly native ground properties); Moderate: Moderate percentage of land disked or used for agriculture; High: High percentage of land disked or used for agriculture.

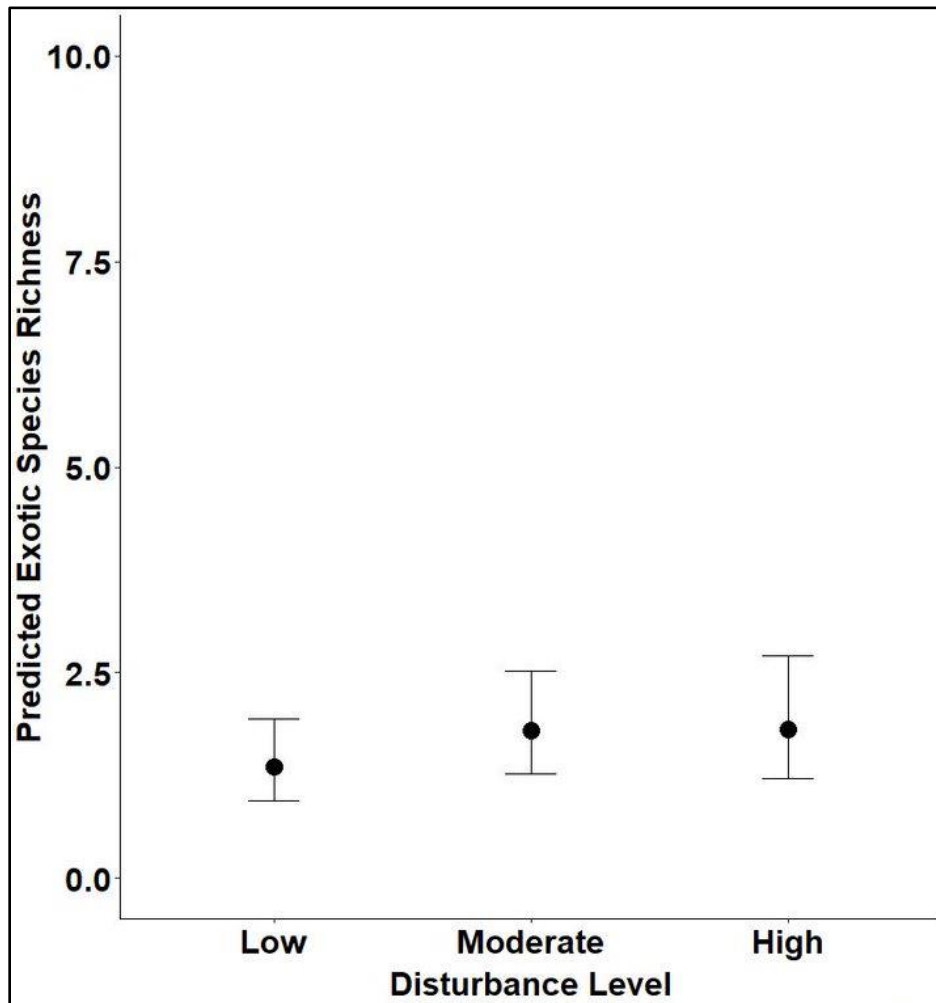
<sup>2</sup>Error bars represent 95% confidence limits.

Figure 3.7. Predicted non-native ant species in relation to the number of RIFA mound for both the Albany and Tallahassee regions. The colored sections represent the confidence limits of the data.<sup>1</sup>



<sup>1</sup>Error bars represent 95% confidence limits.

Figure 3.8. Relationship between the predicted non-native ant species richness and disturbance level.<sup>1,2</sup>



<sup>1</sup>Low: Little to no disking or agriculture (mostly native ground properties); Moderate: Moderate percentage of land disked or used for agriculture; High: High percentage of land disked or used for agriculture.

<sup>2</sup>Error bars represent 95% confidence limits.

Table 3.1. Abbreviations and characteristics for the properties surveyed in my study regions of Albany and Tallahassee during 2016 and 2017.

Year	Region	Property <sup>1</sup>	Groundcover <sup>2</sup>	Burned <sup>3</sup>	Unburned <sup>4</sup>	
2016	Albany	ALB 1	OF	3	3	
		ALB 2	OF	3	3	
		ALB 3	OF	3	3	
	Tallahassee	RH 1	OF	3	3	
		RH 2	OF and NG	6	6	
		RH 3	OF and NG	6	6	
		RH 4	NG	6	0	
		RH 5	NG	3	3	
	2017	Albany	ALB 1	OF	3	3
			ALB 2	OF	3	3
ALB 3			OF	3	3	
ALB 4			NG	3	3	
ALB 5			NG	3	3	
ALB 6			NG	3	3	
Tallahassee		RH 1	OF	3	3	
		RH 2	OF and NG	6	6	
		RH 3	OF and NG	6	6	
		RH 4	NG	6	0	
	RH 5	NG	3	3		

<sup>1</sup> ALB= Albany region; RH= Tallahassee region

<sup>2</sup> OF= Oldfield groundcover; NG= Native groundcover

<sup>3</sup> Number of burned plots

<sup>4</sup> Number of unburned plots



Table 3.2. Variables included in my model suites and *a priori* predictions.

Variable	Prediction
Year	This variable captured year to year variation in both biotic (i.e. predator fluctuation) and abiotic (i.e. changes in weather patterns). I hypothesized that year effects would account for variation not explained by my other variables.
Region	Site can be a source of variation in species assemblages from differences in resource availability habitat suitability and weather. I hypothesized that species assemblages would change due to these regional characteristics.
Burn interval	This variable represented areas that were either burned the year of the surveys (burned) or the previous year (unburned) capturing variation in ant assemblages specifically caused by prescribed fire. I hypothesized that areas more recently burned would have higher numbers of non-native ants.
Number of RIFA foragers	The number of RIFA foragers served to represent the presence of RIFA but did not correlate with the number of RIFA mounds. Therefore this variable was included separately. I hypothesized that higher number of RIFA foragers would increase non-native ant species richness and native ant species richness would decrease.
Number of RIFA mounds	I hypothesized that with higher number of RIFA mounds non-native ant species richness would increase and native ant species richness would decrease.

---

Canopy closure	This variable captured variation in ant assemblages that resulted from difference in canopy closure. I hypothesize that as canopy closure increased non-native ant species richness would decrease and native ant species richness would increase.
Groundcover type	This variable explained variation in ant assemblages due to old field and native groundcover. I hypothesized that old field areas would have higher non-native ant species richness and lower native ant species richness while the reverse would be found in native ground areas.
Disturbance level	This variable categorically captured variation in soil disturbance caused by differing management practices (e.g. annual disking) beyond prescribe fire. I hypothesized that higher levels of disturbance would increase non-native ant and decrease native ant species richness.

---

Table 3.3. Model Suite 1 selection for baseline parameters influencing predicted native ant species richness.

Model parameter	K	AICc	$\Delta$ AICc	$w_i$
Year + Region	5	1256.94	0.00	0.49
Year $\times$ Region	6	1257.98	1.03	0.29
Year	4	1258.57	1.63	0.22
Region	4	1293.01	36.06	0.00

Table 3.4. Model Suite 2 selection for parameters influencing predicted native ant species richness.

Model parameter	K	AICc	$\Delta$ AICc	$w_i$
Number of RIFA mounds $\times$ Region	7	1251.25	0.00	0.33
Number of RIFA mounds	6	1251.37	0.11	0.31
Number of RIFA mounds $\times$ Year	7	1252.14	0.88	0.21
Null (Year + Region)	5	1256.94	5.69	0.02
Number of non-native species	6	1257.29	6.03	0.02
Groundcover $\times$ Region	7	1257.82	6.57	0.01
Groundcover	6	1257.96	6.70	0.01
Number of non-native species $\times$ Region	7	1258.00	6.74	0.01
Disturbance level $\times$ Year	9	1258.07	6.81	0.01
Groundcover $\times$ Year	7	1258.08	6.82	0.01
Burn interval	6	1258.31	7.05	0.01
Disturbance level $\times$ Region	8	1258.45	7.20	0.01
Number of non-native species $\times$ Year	7	1258.46	7.20	0.01
Number of RIFA foragers $\times$ Year	7	1258.94	7.69	0.01
Burn interval $\times$ Region	7	1258.98	7.72	0.01
Number of RIFA foragers	6	1259.02	7.77	0.01
Disturbance level	6	1260.00	8.75	0.00
Burn interval $\times$ Year	7	1260.40	9.15	0.00
Number of RIFA foragers $\times$ Region	7	1261.12	9.86	0.00

Table 3.5. Top model of Suite 2 demonstrate that the number of RIFA mounds has the most weight of all included variables for explaining variation in expected native ant species richness.<sup>1</sup>

Model parameter	No. of candidate models	Sum of importance $w_i$
Number of RIFA mounds	3	0.85
Number of non-native species	3	0.04
Groundcover	3	0.03
Disturbance level	3	0.03
Burn interval	3	0.03
Number of RIFA foragers	3	0.03

<sup>1</sup>All models include Year and Region.

Table 3.6. Estimated effects and Type II likelihood ratio tests for terms included in final Poisson model for number of native ant species at xx sample plots in Florida and Georgia.<sup>1</sup>

Parameter	$\beta$	S.E. <sup>2</sup>	95% C.L. <sup>3</sup>	P
Year	1.37	0.051	1.24, 1.51	1.18e-9*
Region	1.28	0.206	0.833, 1.99	0.236
Albany region				0.003*
with RIFA mound	0.950	0.017	0.919, 0.983	
number				
Tallahassee				0.180
region with RIFA	0.982	0.014	0.956, 1.01	
mound number				

<sup>1</sup>All degrees of freedom = 1.

<sup>2</sup>Standard error.

<sup>3</sup>Confidence limit.

<sup>4</sup>Likelihood ratio test statistic.

\*Statistically significant.

<sup>1</sup> Random effects:  
Property (variance=0.087, standard deviation=0.294), Plot (variance=0.005, standard deviation =0.070)

Table 3.7. Model Suite 1 selection for baseline parameters influencing predicted non-native ant species richness.

Model parameter	K	AICc	$\Delta$ AICc	$w_i$
Year + Region	5	1256.94	0.00	0.49
Year $\times$ Region	6	1257.98	1.03	0.29
Year	4	1258.57	1.63	0.22
Region	4	1293.01	36.06	0.00

Table 3.8. Model Suite 2 selection for parameters influencing predicted non-native ant species richness.

Model parameter	K	AICc	$\Delta$ AICc	$w_i$
Number of RIFA foragers $\times$ Region	7	823.07	0.00	0.86
Groundcover $\times$ Year	7	829.95	6.87	0.03
Disturbance level $\times$ year	9	830.84	7.77	0.02
Burn interval $\times$ Year	7	831.29	8.22	0.01
Number of RIFA foragers	6	831.58	8.51	0.01
Groundcover	6	831.59	8.52	0.01
Number of RIFA mounds	6	832.36	9.29	0.01
Groundcover $\times$ Region	7	832.52	9.45	0.01
Null (Year + Region)	5	832.76	9.69	0.01
Number of RIFA foragers $\times$ Year	7	833.30	10.23	0.01
Number of native species	6	833.31	10.24	0.01
Number of RIFA mounds $\times$ Region	7	833.82	10.75	0.00
Number of RIFA mounds $\times$ Year	7	833.96	10.89	0.00
Burn interval	6	834.46	11.39	0.00
Disturbance level	7	834.91	11.83	0.00
Number of native species $\times$ Region	7	835.40	12.32	0.00
Number of native species $\times$ Year	7	835.42	12.34	0.00
Burn interval $\times$ Region	7	836.06	12.98	0.00
Disturbance level $\times$ Region	8	837.02	13.95	0.00



Table 3.9. Top model of Suite 2 demonstrate that the number of RIFA mounds has the most weight of all included variables for explaining variation in expected native ant species richness.<sup>1</sup>

Model parameter	No. of candidate models	Sum of importance $w_i$
Number of RIFA Foragers	3	0.88
Groundcover	3	0.05
Disturbance level	3	0.02
Burn Interval	3	0.01
Number of native species	3	0.01
Number of RIFA mounds	3	0.01

<sup>1</sup>All models include Year and Region.

Table 3.10. Estimated effects and Type II likelihood ratio tests for terms include in final Poisson model for number of non-native ant species at 78 sample plots in Florida and Georgia.<sup>1</sup>

Parameter	$\beta$	S.E. <sup>2</sup>	95% C.L. <sup>3</sup>	P
Year	1.78	0.105	1.45, 2.19	3.49e-8*
Region	0.433	0.182	0.294, 0.633	4.01e-6*
Albany region with RIFA forager number	1.06	0.094	0.867, 1.26	0.548
Tallahassee region with RIFA forager number	2.19	0.185	1.49, 3.09	2.08e-5*

<sup>1</sup>All degrees of freedom = 1.

<sup>2</sup>Standard error.

<sup>3</sup>Confidence limit.

\*Statistically significant.

## **Chapter 4: Synthesis and conclusions**

Overall, my first hypothesis was partially supported and my second hypothesis was fully supported. Expected RIFA density was influenced by region and other environmental variables, including survey year and burn interval. Higher mound numbers were found the Albany region, areas that had not been burned in a year, and 2017. Regionally, this result correlates with higher rates of bobwhite nest depredation seen in the Albany (Haines et al. 2017). I was expecting areas more recently burned to have higher RIFA numbers, but they could need several months to establish colonies after a burn clears vegetation from an area. In terms of year, it could be that RIFA colonies were not doing well in 2016 as it was a drought year with high temperatures, and RIFA tend to be sensitive to low moisture and extreme temperatures.

For local ant assemblages, my hypothesis that RIFA would impact both native and non-native ant species richness was supported. Native ant species richness decreased, which makes sense due to the aggressive nature of RIFAs and past research supporting the argument that they are drivers of biodiversity loss. I found it interesting that higher RIFA presence correlated with higher non-native ant species richness. This relationship could mean that RIFAs and other non-native ants are taking advantage of similar environmental variables to invade. This relationship could also mean that non-native ants are more competitive than natives, or perhaps exploit different resources so that there is less competition with RIFA.

### **Future Research**

In relation to my mound research, more work needs to be done to isolate what about “Region” is influencing RIFA density. Including a climate variable, such as the Keetch-Byram

Drought Index, could be helpful. I also wish to quantify disturbance levels beyond generic categories and include annual disking percentages in my analysis. Further research should also be done to isolate the influence of RIFA on local ant communities. Setting up experimental plots where RIFA are controlled with boiling water and not chemicals, which could kill other ant species, quantify how an ant community changes over time when not competing with RIFA. Over time, this could also be used to see how quickly native ant communities can recover from competition with RIFA. On a larger scale, using study sites with a wider range of disturbance, climate, and soil would determine their respective influence on RIFA density and impacts in other regions. Building upon our understanding of RIFA invasion is important, as RIFA are gradually expanding their range northward with climate change (Morrison et al. 2005). Not only that, but there is a deficit of research quantifying how invasive invertebrates impact native invertebrates. This is quite the gap of knowledge, especially considering that approximately 1.1 million known arthropods (predominantly insects) make up half of the described species on Earth (Hawksworth and Kalin-Arroyo 1995, Hamilton et al. 2010). Native invertebrates also provide important ecosystem services such as seed dispersal (Heithaus 1981, Kalisz et al. 1999), decomposition (Lavelle et al. 2006), and soil aeration (Stork and Eggleton 1992). If these native invertebrates are displaced by invasive invertebrates, it is possible that ecosystem services will be lost (Zettler et al. 2001, Stuble et al. 2005). The potential loss of ecosystem services, as well as potential loss of biodiversity, warrants more research into relationships of competing invasive and native invertebrates.

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## APPENDIX 1: RESULTS OF DISTANCE ANALYSIS

Appendix Table 1.1. Distance analysis of variables to estimate impairment of RIFA mound detection.

Key function	Covariate Model	Est P <sup>1</sup>	SE (P) <sup>2</sup>	Δ_AIC
Hazard-rate	~Height + factor(Year)	0.7	0.06	0
Hazard-rate	~Height + Ground.cover + factor(Year)	0.7	0.07	1.88
Hazard-rate	~Height + Fire.Type + factor(Year)	0.7	0.06	1.97
Hazard-rate	~factor(Year)	0.68	0.07	2.36
Hazard-rate	~Ground.cover * factor(Year)	0.62	0.12	3.51
Hazard-rate	~Height + Fire.Type + Ground.cover + factor(Year)	0.7	0.07	3.87
Hazard-rate	~Fire.Type + factor(Year)	0.68	0.08	4.01
Hazard-rate	~Ground.cover + factor(Year)	0.67	0.08	4.22
Half-normal	~factor(Year)	0.73	0.03	5.45
Hazard-rate	~Fire.Type + Ground.cover + factor(Year)	0.66	0.08	5.79
Hazard-rate	~Fire.Type * factor(Year)	0.68	0.08	6.01
Half-normal	~Ground.cover + factor(Year)	0.73	0.03	7.34
Half-normal	~Fire.Type + factor(Year)	0.73	0.03	7.43

Half-normal	~Ground.cover * factor(Year)	0.73	0.03	9.07
Half-normal	~Fire.Type + Ground.cover + factor(Year)	0.73	0.03	9.3
Hazard-rate	~Ground.cover	0.69	0.07	9.69
Uniform with cosine adjustment term of order 1	None	0.71	0.03	9.76
Half-normal	None	0.73	0.03	10.04
Half-normal	~Ground.cover	0.73	0.03	10.76
Hazard-rate	~Height + Ground.cover	0.7	0.07	11
Hazard-rate	None	0.71	0.06	11.41
Hazard-rate	~Fire.Type + Ground.cover	0.68	0.08	11.43
Half-normal	~Fire.Type	0.73	0.03	11.99
Hazard-rate	~Height	0.72	0.06	12.4
Hazard-rate	~Fire.Type * Ground.cover	0.68	0.07	12.56
Hazard-rate	~Height + Fire.Type + Ground.cover	0.69	0.07	12.71
Half-normal	~Fire.Type + Ground.cover	0.73	0.03	12.75
Hazard-rate	~Height * Ground.cover	0.7	0.07	12.8
Hazard-rate	~Fire.Type	0.7	0.07	13.34
Hazard-rate	~Height + Fire.Type	0.72	0.06	14.36

<sup>1</sup>Est P = average detection probability.

<sup>2</sup>SE (P) = standard error of average detection probability.



## APPENDIX 2: R CODE

---

### *Chapter 2*

---

```
#refit final model for mound analysis excluding soil variables

library(lme4)

library(blme4)

library(car)

mound.fixedburn=read.csv(file.choose())

head(mound.fixedburn)

mound.fixedburn$Year=factor(mound.fixedburn$Year)

mound.fixedburn$Year

mound.fixedburn$Canopy.Cover=mound.fixedburn$Canopy.Cover/100

mound.fixedburn$Canopy.Cover

mound.fixedburn$DistCAT <- factor(mound.fixedburn$Dist.lvl,levels=c("Low","Mod","High"))

mound.fixedburn$DistCAT

model.refit= (glmer(Total.Mounds~Year+Ground.cover+DistCAT+Year/Ground.cover
                    +Year/Fire.Type+Year/Canopy.Cover+Region+(1|Plantation)+(1|Plot.name),
                    family=poisson,data=mound.fixedburn,control=glmerControl(optimizer="bobyqa")))

summary(model.refit)

Anova(model.refit)
```

```
model.refit.conf=confint(model.refit)
```

```
-----
```

```
#for canopy closure coef, to balance scaling
```

```
exp(0.1*coef(summary(model.refit))[,1])
```

```
exp(0.1* model.refit.conf)#for everything else
```

```
exp(coef(summary(model.refit))[,1])
```

```
exp(model.refit.conf)
```

```
exp(ranef(model.refit)$Plantation)
```

```
-----
```

```
#models for mound analysis including soil variables
```

```
-----
```

```
#D1.sand
```

```
mound.soil$D1.Sand=mound.soil$D1.Sand/100
```

```
mound.soil$D1.Sand
```

```
model.soild1sand=
```

```
(glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover+DistCAT
```

```
  +D1.Sand+Year:Fire.Type+Year:Canopy.Cover+(1|Plantation)+(1|Plot.name),
```

```
  family=poisson,data=mound.soil,control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild1sand)
```

```
-----
```

```
#D2.sand
```

```
mound.soil$D2.Sand=mound.soil$D2.Sand/100
```

```
mound.soil$D2.Sand
```

```
model.soild2sand=(glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover
+Canopy.Cover+DistCAT+D2.Sand+Year:Fire.Type+Year:Canopy.Cover+(1|Plantation)
+(1|Plot.name),family=poisson,data=mound.soil,
control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild2sand)
```

-----

```
#D1.clay
```

```
mound.soil$D1.Clay=mound.soil$D1.Clay/100
```

```
mound.soil$D1.Clay
```

```
model.soild1clay=(glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover
+DistCAT+D1.Clay+Year:Fire.Type+Year:Canopy.Cover+(1|Plantation)+(1|Plot.name),
family=poisson,data=mound.soil,control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild1clay)
```

-----

```
#D2.clay
```

```
mound.soil$D2.Clay=mound.soil$D2.Clay/100
```

```
mound.soil$D2.Clay
```

```
model.soild2clay=(glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover
+DistCAT+D2.Clay+Year:Fire.Type+Year:Canopy.Cover+(1|Plantation)+(1|Plot.name),
family=poisson,data=mound.soil,control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild2clay)
```

-----

```
#D1.pH
```

```
model.soild1pH= (glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover
+DistCAT+D1.pH+Year:Fire.Type+Year:Canopy.Cover+(1|Plantation)+(1|Plot.name),
family=poisson,data=mound.soil,control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild1pH)
```

-----

```
#D2.pH
```

```
model.soild2pH= (glmer(Total.Mounds~Year+Ground.cover+Fire.Type+Canopy.Cover
+DistCAT D2.pH+Year:Fire.Type+Year:Canopy.Cover+Region+(1|Plantation)
+(1|Plot.name),family=poisson,data=mound.soil,
control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild2pH)
```

-----

```
#D1.BD
```

```
model.soild1BD= (glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover
+DistCAT+D1.BD+Year:Fire.Type+Year:Canopy.Cover+Region+(1|Plantation)
+(1|Plot.name),family=poisson,data=mound.soil,
control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.soild1BD)
```

-----

```
#D2.BD
```

```
model.soild2BD= (glmer(Total.Mounds~Year+Region+Fire.Type+Ground.cover+Canopy.Cover
+DistCAT+D2.BD+Year:Fire.Type+Year:Canopy.Cover+Region+(1|Plantation)
+(1|Plot.name),family=poisson,data=mound.soil,
```

```
control=glmerControl(optimizer="bobyqa"))
summary(model.soild2BD)
```

---

### *Chapter 3*

---

```
library(lme4)
library(blme4)
library(car)
library(AICcmodavg)
pitfall.guild=read.csv(file.choose())
head(pitfall.guild)
pitfall.guild$Year=factor(pitfall.guild$Year)
pitfall.guild$Year
#pitfall.guild$Canopy.Cover=pitfall.guild$Canopy.Cover*100
pitfall.guild$Canopy.Cover=pitfall.guild$Canopy.Cover/100
pitfall.guild$Canopy.Cover
pitfall.guild$RegionYear=factor(with(pitfall.guild,paste(Region,Year,sep="")))
mound.fixedburn$DistCAT <- factor(mound.fixedburn$Dist.lvl,levels=c("Low","Mod","High"))
mound.fixedburn$DistCAT
```

---

```
#Native ant species number analysis
```

---

```
#MS1.1: intercept only
```

```
model.MS1.1= (glmer(Native.sp~offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.MS1.1)
```

```
dispersion_glmer(model.MS1.1)
```

```
model.MS1.1.conf=confint(model.MS1.1)
```

```
model.MS1.1.conf
```

```
exp(coef(summary(model.MS1.1))[,1])
```

```
exp(model.MS1.1.conf)
```

-----

```
#MS1.2: year
```

```
model.MS1.2= (glmer(Native.sp~Year+offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.MS1.2)
```

```
dispersion_glmer(model.MS1.2)
```

```
model.MS1.2.conf=confint(model.MS1.2)
```

```
model.MS1.2.conf
```

```
exp(coef(summary(model.MS1.2))[,1])
```

```
exp(model.MS1.2.conf)
```

-----

```
#MS1.3: region
```

```
model.MS1.3= (glmer(Native.sp~Region+offset(log(Func.Trap.No))
```

```

      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
      control=glmerControl(optimizer="bobyqa"))

summary(model.MS1.3)

dispersion_glmer(model.MS1.3)

model.MS1.3.conf=confint(model.MS1.3)

model.MS1.3.conf

exp(coef(summary(model.MS1.3))[,1])

exp(model.MS1.3.conf)

```

```

-----

#model.MS1.4: year and region

model.MS1.4= (glmer(Native.sp~Year+Region+offset(log(Func.Trap.No))
      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
      control=glmerControl(optimizer="bobyqa"))

summary(model.MS1.4)

dispersion=glmer(model.MS1.4)

model.MS1.4.conf=confint(model.MS1.4)

model.MS1.4.conf

exp(coef(summary(model.MS1.4))[,1])

exp(model.MS1.4.conf)

```

```

-----

#model.MS1.5: year, region, and Year*Region

model.MS1.5= (glmer(Native.sp~Year*Region+offset(log(Func.Trap.No))
      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,

```

```

        control=glmerControl(optimizer="bobyqa"))

summary(model.MS1.5)

dispersion_glmer(model.MS1.5)

model.MS1.5.conf=confint(model.MS1.5)

model.MS1.5.conf

exp(coef(summary(model.MS1.5))[,1])

exp(model.MS1.5.conf)

-----

#model.MS1.6: add in native species individuals

model.MS1.6= (glmer(Native.sp~Scaled.Native.no+offset(log(Func.Trap.No))
        +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
        control=glmerControl(optimizer="bobyqa"))

summary(model.MS1.6)

dispersion_glmer(model.MS1.6)

model.MS1.6.conf=confint(model.MS1.6)

model.MS1.6.conf

exp(coef(summary(model.MS1.6))[,1])

exp(model.MS1.6.conf)

-----

#model.MS1.7: add in native species individuals

model.MS1.7= (glmer(Native.sp~Year+Region+Scaled.Native.no+offset(log(Func.Trap.No))
        +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
        control=glmerControl(optimizer="bobyqa"))

```



```

summary(model.MS1.7)

dispersion_glmer(model.MS1.7)

model.MS1.7.conf=confint(model.MS1.7)

model.MS1.7.conf

exp(coef(summary(model.MS1.7))[,1])

exp(model.MS1.7.conf)

-----

#MS1: aic1

Modnames1 <- c("B0","Year","Region","Year+Region","Year*Region")

aictab(c(model.MS1.1,model.MS1.2,model.MS1.3,model.MS1.4,model.MS1.5), Modnames1,
data=pitfall.guild)

-----

#model.MS2.1a: created intercept only

model.MS2.1a= (glmer(Native.sp~Year+Region+offset(log(Func.Trap.No))
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.1a)

dispersion_glmer(model.MS2.1a)

model.MS2.1a.conf=confint(model.MS2.1a)

model.MS2.1a.conf

exp(coef(summary(model.MS2.1a))[,1])

exp(model.MS2.1a.conf)

-----

```

```

#model.MS2.1b: add in groundcover

model.MS2.1b= (glmer(Native.sp~Year+Region+Ground.cover+offset(log(Func.Trap.No))
                    +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                    control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.1b)

dispersion_glmer(model.MS2.1b)

model.MS2.1b.conf=confint(model.MS2.1b)

model.MS2.1b.conf

exp(coef(summary(model.MS2.1b))[,1])

exp(model.MS2.1b.conf)

-----

#model.MS2.2: add Ground.cover*Year

model.MS2.2= (glmer(Native.sp~Year+Region+Ground.cover*Year+offset(log(Func.Trap.No))
                    +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                    control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.2)

dispersion_glmer(model.MS2.2)

model.MS2.2.conf=confint(model.MS2.2)

model.MS2.2.conf

exp(coef(summary(model.MS2.2))[,1])

exp(model.MS2.2.conf)

-----

#model.MS2.3: add Ground.cover *Region

```

```

model.MS2.3= (glmer(Native.sp~Year+Region+Ground.cover*Region+
                offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),family=poisson,
                data=pitfall.guild,control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.3)

dispersion_glmer(model.MS2.3)

model.MS2.3.conf=confint(model.MS2.3)

model.MS2.3.conf

exp(coef(summary(model.MS2.3))[,1])

exp(model.MS2.3.conf)

-----

#model.MS2.4: add in Fire.type

model.MS2.4= (glmer(Native.sp~Year+Region+Fire.Type+offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.4)

dispersion_glmer(model.MS2.4)

model.MS2.4.conf=confint(model.MS2.4)

model.MS2.4.conf

exp(coef(summary(model.MS2.4))[,1])

exp(model.MS2.4.conf)

-----

#model.MS2.5: add in Fire.type*Year

model.MS2.5= (glmer(Native.sp~Year+Region+Fire.Type*Year+offset(log(Func.Trap.No))

```

```

      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
      control=glmerControl(optimizer="bobyqa"))))

summary(model.MS2.5)

dispersion_glmer(model.MS2.5)

model.MS2.5.conf=confint(model.MS2.5)

model.MS2.5.conf

exp(coef(summary(model.MS2.5))[,1])

exp(model.MS2.5.conf)

-----

#model.MS2.6: add in Fire.type*Region

model.MS2.6= (glmer(Native.sp~Year+Region+Fire.Type*Region+offset(log(Func.Trap.No))
      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
      control=glmerControl(optimizer="bobyqa"))))

summary(model.MS2.6)

dispersion=glmer(model.MS2.6)

model.MS2.6.conf=confint(model.MS2.6)

model.MS2.6.conf

exp(coef(summary(model.MS2.6))[,1])

exp(model.MS2.6.conf)

-----

#model.MS2.7: add in Scaled.RIFA.no

model.MS2.7= (glmer(Native.sp~Year+Region+Scaled.RIFA.no+offset(log(Func.Trap.No))
      +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,

```

```

control=glmerControl(optimizer="bobyqa"))

summary(model.MS2.7)

dispersion=glmer(model.MS2.7)

model.MS2.7.conf=confint(model.MS2.7)

model.MS2.7.conf

exp(coef(summary(model.MS2.7))[,1])

exp(model.MS2.7.conf)

-----

#model.MS2.8: add in Scaled.RIFA.no*Year

model.MS2.8= (glmer(Native.sp~Year+Region+Scaled.RIFA.no*Year+
  offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),family=poisson,
  data=pitfall.guild,control=glmerControl(optimizer="bobyqa"))

summary(model.MS2.8)

dispersion_glmer(model.MS2.8)

model.MS2.8.conf=confint(model.MS2.8)

model.MS2.8.conf

exp(coef(summary(model.MS2.8))[,1])

exp(model.MS2.8.conf)

-----

#model.MS2.9: add in Scaled.RIFA.no*Region

model.MS2.9= (glmer(Native.sp~Year+Region+Scaled.RIFA.no*Region+
  offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),family=poisson,
  data=pitfall.guild, control=glmerControl(optimizer="bobyqa"))

summary(model.MS2.9)

```

```

dispersion_glmer(model.MS2.9)

model.MS2.9.conf=confint(model.MS2.9)

model.MS2.9.conf

exp(coef(summary(model.MS2.9))[,1])

exp(model.MS2.9.conf)

-----

#model.MS2.10: add in Mounds

model.MS2.10= (glmer(Native.sp~Year+Region+Total.Mounds+offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.10)

dispersion_glmer(model.MS2.10)

model.MS2.10.conf=confint(model.MS2.10)

model.MS2.10.conf

exp(coef(summary(model.MS2.10))[,1])

exp(model.MS2.10.conf)

-----

#model.MS2.11: add in Mounds*Year

model.MS2.11= (glmer(Native.sp~Year+Region+Total.Mounds*Year+
                    offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),family=poisson,
                    data=pitfall.guild, control=glmerControl(optimizer="bobyqa")))

summary(model.MS2.11)

dispersion_glmer(model.MS2.11)

```

```
model.MS2.11.conf=confint(model.MS2.11)
```

```
model.MS2.11.conf
```

```
exp(coef(summary(model.MS2.11))[,1])
```

```
exp(model.MS2.11.conf)
```

```
-----
```

```
#model.MS2.12: add in Mounds*Region
```

```
model.MS2.12= (glmer(Native.sp~Year+Region+Total.Mounds*Region+  
  offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),family=poisson,  
  data=pitfall.guild,control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.MS2.12)
```

```
dispersion=glmer(model.MS2.12)
```

```
model.MS2.12.conf=confint(model.MS2.12)
```

```
model.MS2.12.conf
```

```
exp(coef(summary(model.MS2.12))[,1])
```

```
exp(model.MS2.12.conf)
```

```
-----
```

```
#add model with non-native sp richness as a covariate
```

```
#model.MS2.13: add in Exotic.sp
```

```
model.MS2.12= (glmer(Native.sp~Year+Region+Exotic.sp+offset(log(Func.Trap.No))  
  +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,  
  control=glmerControl(optimizer="bobyqa")))
```

```
summary(model.MS2.12)
```

```
dispersion_glmer(model.MS2.12)
```

```
model.MS2.12.conf=confint(model.MS2.12)
```

```
model.MS2.12.conf
```

```
exp(coef(summary(model.MS2.12))[,1])
```

```
exp(model.MS2.12.conf)
```

```
-----  
#MS2: aic2
```

```
Modnames2 <- c("Groundc", "Groundc*Year", "Groundc*Region", "Fire.Type",  
"Fire.Type*Year", "Fire.Type+Region", "RIFA.no", "RIFA.no*Year", "RIFA.no*Region",  
"Mound.no", "Mound.no*Year", "Mound.no*Region")
```

```
aictab(c(model.MS2.1a, model.MS2.1b, model.MS2.2, model.MS2.3, model.MS2.4, model.MS2.5,  
model.MS2.6, model.MS2.7, model.MS2.8, model.MS2.9, model.MS2.10, model.MS2.11,  
model.MS2.12), Modnames2, data=pitfall.guild)
```

```
-----  
#Non-native ant species number analysis  
-----
```

```
#MS1.1: intercept only
```

```
exoticMS1.1= (glmer(Exotic.sp~offset(log(Func.Trap.No))  
+(1|Plantation)+(1|Plot.name), family=poisson, data=pitfall.guild,  
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.1)
```

```
dispersion_glmer(exoticMS1.1)
```

```
exoticMS1.1.conf=confint(exoticMS1.1)
```

```
exoticMS1.1.conf
```



```
exp(coef(summary(exoticMS1.1))[,1])
```

```
exp(exoticMS1.1.conf)
```

```
-----
```

```
#MS1.2: year
```

```
exoticMS1.2= (glmer(Exotic.sp~Year+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.2)
```

```
dispersion_glmer(exoticMS1.2)
```

```
exoticMS1.2.conf=confint(exoticMS1.2)
```

```
exoticMS1.2.conf
```

```
exp(coef(summary(exoticMS1.2))[,1])
```

```
exp(exoticMS1.2.conf)
```

```
-----
```

```
#MS1.3: region
```

```
exoticMS1.3= (glmer(Exotic.sp~Region+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.3)
```

```
dispersion_glmer(exoticMS1.3)
```

```
exoticMS1.3.conf=confint(exoticMS1.3)
```

```
exoticMS1.3.conf
```

```
exp(coef(summary(exoticMS1.3))[,1])
```

```
exp(exoticMS1.3.conf)
```

```
-----
```

```
#exoticMS1.4: year and region
```

```
exoticMS1.4= (glmer(Exotic.sp~Year+Region+offset(log(Func.Trap.No))  
              +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,  
              control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.4)
```

```
dispersion_glmer(exoticMS1.4)
```

```
exoticMS1.4.conf=confint(exoticMS1.4)
```

```
exoticMS1.4.conf
```

```
exp(coef(summary(exoticMS1.4))[,1])
```

```
exp(exoticMS1.4.conf)
```

```
-----
```

```
#exoticMS1.5: year, region, and Year*Region
```

```
exoticMS1.5= (glmer(Exotic.sp~Year*Region+offset(log(Func.Trap.No))  
              +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,  
              control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.5)
```

```
dispersion_glmer(exoticMS1.5)
```

```
exoticMS1.5.conf=confint(exoticMS1.5)
```

```
exoticMS1.5.conf
```

```
exp(coef(summary(exoticMS1.5))[,1])
```

```
exp(exoticMS1.5.conf)
```

---

#exoticMS1.6: add in native species individuals

```
exoticMS1.6= (glmer(Exotic.sp~Scaled.Native.no+offset(log(Func.Trap.No))
              +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
              control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.6)
```

```
dispersion_glmer(exoticMS1.6)
```

```
exoticMS1.6.conf=confint(exoticMS1.6)
```

```
exoticMS1.6.conf
```

```
exp(coef(summary(exoticMS1.6))[,1])
```

```
exp(exoticMS1.6.conf)
```

---

#exoticMS1.7: add in native species individuals

```
exoticMS1.7= (glmer(Exotic.sp~Year+Region+Scaled.Native.no+offset(log(Func.Trap.No))
                  +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                  control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS1.7)
```

```
dispersion_glmer(exoticMS1.7)
```

```
exoticMS1.7.conf=confint(exoticMS1.7)
```

```
exoticMS1.7.conf
```

```
exp(coef(summary(exoticMS1.7))[,1])
```

```
exp(exoticMS1.7.conf)
```

---

```

#MS1: aic1

Modnames <- c("B0","Year","Region","Year+Region","Year*Region")

aictab(c(model.MS1.1,model.MS1.2,model.MS1.3,model.MS1.4,model.MS1.5), Modnames,
data=pitfall.guild)

#model.MS2.1a: created intercept only

-----

exoticMS2.1a= (glmer(Exotic.sp~Year+Region+offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))

summary(exoticMS2.1a)

dispersion_glmer(exoticMS2.1a)

exoticMS2.1a.conf=confint(exoticMS2.1a)

exoticMS2.1a.conf

exp(coef(summary(exoticMS2.1a))[,1])

exp(exoticMS2.1a.conf)

-----

#exoticMS2.1b: add in groundcover

exoticMS2.1b= (glmer(Exotic.sp~Year+Region+Ground.cover+offset(log(Func.Trap.No))
                +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
                control=glmerControl(optimizer="bobyqa")))

summary(exoticMS2.1b)

dispersion_glmer(exoticMS2.1b)

exoticMS2.1b.conf=confint(exoticMS2.1b)

```

```
exoticMS2.1b.conf
```

```
exp(coef(summary(exoticMS2.1b))[,1])
```

```
exp(exoticMS2.1b.conf)
```

```
-----
```

```
#exoticMS2.2: add Ground.cover*Year
```

```
exoticMS2.2= (glmer(Exotic.sp~Year+Region+Ground.cover*Year+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.2)
```

```
dispersion_glmer(exoticMS2.2)
```

```
exoticMS2.2.conf=confint(exoticMS2.2)
```

```
exoticMS2.2.conf
```

```
exp(coef(summary(exoticMS2.2))[,1])
```

```
exp(exoticMS2.2.conf)
```

```
-----
```

```
#exoticMS2.3: add Ground.cover*Region
```

```
exoticMS2.3= (glmer(Exotic.sp~Year+Region+Ground.cover*Region+
```

```
offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),
```

```
family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.3)
```

```
dispersion_glmer(exoticMS2.3)
```

```
exoticMS2.3.conf=confint(exoticMS2.3)
```

```
exoticMS2.3.conf
```

```
exp(coef(summary(exoticMS2.3))[,1])
```

```
exp(exoticMS2.3.conf)
```

```
-----
```

```
#exoticMS2.4: add in Fire.type
```

```
exoticMS2.4= (glmer(Exotic.sp~ Year+Region+Fire.Type+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.4)
```

```
dispersion_glmer(exoticMS2.4)
```

```
exoticMS2.4.conf=confint(exoticMS2.4)
```

```
exoticMS2.4.conf
```

```
exp(coef(summary(exoticMS2.4))[,1])
```

```
exp(exoticMS2.4.conf)
```

```
-----
```

```
#exoticMS2.5: add in Fire.type*Year
```

```
exoticMS2.5= (glmer(Exotic.sp~ Year+Region+Fire.Type*Year+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.5)
```

```
dispersion_glmer(exoticMS2.5)
```

```
exoticMS2.5.conf=confint(exoticMS2.5)
```

```
exoticMS2.5.conf
```

```
exp(coef(summary(exoticMS2.5))[,1])
```

```
exp(exoticMS2.5.conf)
```

```
-----
```

```
#exoticMS2.6: add in Fire.type*Region
```

```
exoticMS2.6= (glmer(Exotic.sp~Year+Region+Fire.Type*Region+offset(log(Func.Trap.No))
```

```
+ (1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.6)
```

```
dispersion_glmer(exoticMS2.6)
```

```
exoticMS2.6.conf=confint(exoticMS2.6)
```

```
exoticMS2.6.conf
```

```
exp(coef(summary(exoticMS2.6))[,1])
```

```
exp(exoticMS2.6)
```

```
-----
```

```
#exoticMS2.7: add in Scaled.RIFA.no
```

```
exoticMS2.7= (glmer(Exotic.sp~Year+Region+Scaled.RIFA.no+offset(log(Func.Trap.No))
```

```
+ (1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.7)
```

```
dispersion_glmer(exoticMS2.7)
```

```
exoticMS2.7.conf=confint(exoticMS2.7)
```

```
exoticMS2.7.conf
```

```
exp(coef(summary(exoticMS2.7))[,1])
```

```
exp(exoticMS2.7.conf)
```

---

```
#exoticMS2.8: add in Scaled.RIFA.no*Year
```

```
exoticMS2.8= (glmer(Exotic.sp~Year+Region+Scaled.RIFA.no*Year+  
  offset(log(Func.Trap.No))+(1|Plantation)+(1|Plot.name),  
  family=poisson,data=pitfall.guild,  
  control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.8)
```

```
dispersion_glmer(exoticMS2.8)
```

```
exoticMS2.8.conf=confint(exoticMS2.8)
```

```
exoticMS2.8.conf
```

```
exp(coef(summary(exoticMS2.8))[,1])
```

```
exp(exoticMS2.8.conf)
```

---

```
#exoticMS2.9: add in Scaled.RIFA.no*Region
```

```
exoticMS2.9=
```

```
(glmer(Exotic.sp~Year+Region+Scaled.RIFA.no*Region+offset(log(Func.Trap.No))  
  +(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,  
  control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.9)
```

```
dispersion_glmer(exoticMS2.9)
```

```
exoticMS2.9.conf=confint(exoticMS2.9)
```

```
exoticMS2.9.conf
```



```
exp(coef(summary(exoticMS2.9))[,1])
```

```
exp(exoticMS2.9.conf)
```

```
-----
```

```
#exoticMS2.10: add in Mounds
```

```
exoticMS2.10= (glmer(Exotic.sp~Year+Region+Total.Mounds+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.10)
```

```
dispersion_glmer(exoticMS2.10)
```

```
exoticMS2.10.conf=confint(exoticMS2.10)
```

```
exoticMS2.10.conf
```

```
exp(coef(summary(exoticMS2.10))[,1])
```

```
exp(exoticMS2.10.conf)
```

```
-----
```

```
#exoticMS2.11: add in Mounds*Year
```

```
exoticMS2.11= (glmer(Exotic.sp~Year+Region+Total.Mounds*Year+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.11)
```

```
dispersion_glmer(exoticMS2.11)
```

```
exoticMS2.11.conf=confint(exoticMS2.11)
```

```
exoticMS2.11.conf
```

```
exp(coef(summary(exoticMS2.11))[,1])
```

```
exp(exoticMS2.11.conf)
```

-----

```
#exoticMS2.12: add in Mounds*Region
```

```
exoticMS2.12=
```

```
(glmer(Exotic.sp~Year+Region+Total.Mounds*Region+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.12)
```

```
dispersion_glmer(exoticMS2.12)
```

```
exoticMS2.12.conf=confint(exoticMS2.12)
```

```
exoticMS2.12.conf
```

```
exp(coef(summary(exoticMS2.12))[,1])
```

```
exp(exoticMS2.12.conf)
```

-----

```
#add model with exotic sp richness as a covariate
```

```
#exoticMS2.13: add in Native.sp
```

```
exoticMS2.13= (glmer(Exotic.sp~Year+Region+Native.sp+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.13)
```

```
dispersion_glmer(exoticMS2.13)
```

```
exoticMS2.13.conf=confint(exoticMS2.13)
```

```
exoticMS2.13.conf
```

```
exp(coef(summary(exoticMS2.13))[,1])
```

```
exp(exoticMS2.13.conf)
```

```
-----
```

```
#exoticMS2.14: add in Native.sp*Year
```

```
exoticMS2.14= (glmer(Exotic.sp~Year+Region+Native.sp*Year+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.14)
```

```
dispersion_glmer(exoticMS2.14)
```

```
exoticMS2.14.conf=confint(exoticMS2.14)
```

```
exoticMS2.14.conf
```

```
exp(coef(summary(exoticMS2.14))[,1])
```

```
exp(exoticMS2.14.conf)
```

```
-----
```

```
#exoticMS2.15: add in Native.sp*Region
```

```
exoticMS2.15= (glmer(Exotic.sp~Year+Region+Native.sp*Region+offset(log(Func.Trap.No))
```

```
+(1|Plantation)+(1|Plot.name),family=poisson,data=pitfall.guild,
```

```
control=glmerControl(optimizer="bobyqa")))
```

```
summary(exoticMS2.15)
```

```
dispersion_glmer(exoticMS2.15)
```

```
exoticMS2.15.conf=confint(exoticMS2.15)
```

```
exoticMS2.15.conf
```

```
exp(coef(summary(exoticMS2.15))[,1])
```

```
exp(exoticMS2.15.conf)
```

```
-----  
#MS2: aic2
```

```
Modnames2 <- c("Intercept", "Groundc", "Groundc*Year", "Groundc*Region", "Fire.Type",  
"Fire.Type*Year", "Fire.Type+Region", "RIFA.no", "RIFA.no*Year", "RIFA.no*Region",  
"Mound.no", "Mound.no*Year", "Mound.no*Region", "Native", "Native*Year",  
"Native*Region")
```

```
aictab(c(exoticMS2.1a,exoticMS2.1b,exoticMS2.2,exoticMS2.3,exoticMS2.4,exoticMS2.5,  
exoticMS2.6,exoticMS2.7,exoticMS2.8,exoticMS2.9,exoticMS2.10,exoticMS2.11,  
exoticMS2.12,exoticMS2.13,exoticMS2.14,exoticMS2.15), Modnames2, data=pitfall.guild)
```

### APPENDIX 3: SOIL RESULTS FOR CHAPTER 2

Appendix Table 3.1. Results from adding each relevant soil variable individually to my final Poisson model.

Parameter	$\beta$	S.E. <sup>1</sup>	95% C.L. <sup>3</sup>	P
D1 Sand percentage	-1.47	2.69	-7.00, 4.03	0.584
D2 Sand percentage	-1.43	1.01	-3.52, 0.608	0.156
D1 Clay percentage	-0.980	4.12	-9.49, 7.37	0.812
D2 Clay percentage	1.43	1.05	-0.688, 3.60	0.172
D1 pH	-0.669	0.339	-1.33, -0.004	0.049
D2 pH	-0.598	0.499	-1.58, 0.381	0.231
D1 Bulk Density	0.168	0.723	-1.27, 1.70	0.816
D2 Bulk Density	0.044	0.665	-1.24, 1.54	0.947

<sup>1</sup>Standard error

<sup>2</sup>Confidence limit

\*Statistically significant

## APPENDIX 4: ANT SPECIES IN CHAPTER 3

Appendix Table 4.1. Taxonomic list of ant species found in pitfall surveys taken in 2016 and 2017.

Sub-family	Genus	Species
Dolichoderinae	Dorymyrmex	bureni
Dolichoderinae	Dorymyrmex	flavopectus
Dolichoderinae	Dorymyrmex	grandulus
Dolichoderinae	Dorymyrmex	reginicula
Dolichoderinae	Forelius	pruinosis
Dorylinae	Neivamyrmex	opacithorax
Ectatomminae	Gnamptogenys	triangularis
Formicinae	Brachymyrmex	depilis
Formicinae	Brachymyrmex	obscurior
Formicinae	Brachymyrmex	patagonicus
Formicinae	Camponotus	castaneus
Formicinae	Camponotus	floridanus
Formicinae	Camponotus	sexguttatus
Formicinae	Formica	archboldi
Formicinae	Formica	biophilica
Formicinae	Formica	dolosa

Formicinae	Nylanderia	arenivaga
Formicinae	Nylanderia	concinna
Formicinae	Nylanderia	faisonensis
Formicinae	Nylanderia	parvula
Formicinae	Nylanderia	phantasma
Formicinae	Nylanderia	querna
Formicinae	Nylanderia	sp.
Formicinae	Nylanderia	trageri
Formicinae	Nylanderia	vividula
Formicinae	Nylanderia	wojciki
Myrmicinae	Aphaenogaster	ashmeadi
Myrmicinae	Aphaenogaster	carolinensis
Myrmicinae	Aphaenogaster	flemingi
Myrmicinae	Aphaenogaster	fulva
Myrmicinae	Aphaenogaster	miamiana
Myrmicinae	Aphaenogaster	picea
Myrmicinae	Aphaenogaster	rudis
Myrmicinae	Aphaenogaster	texana
Myrmicinae	Aphaenogaster	treatae
Myrmicinae	Cardiocondyla	wroughtonii
Myrmicinae	Crematogaster	ashmeadi
Myrmicinae	Crematogaster	atkinsoni
Myrmicinae	Crematogaster	lineolata

Myrmicinae	Crematogaster	minutissima
Myrmicinae	Crematogaster	missuriensis
Myrmicinae	Crematogaster	pilosa
Myrmicinae	Crematogaster	pinicola
Myrmicinae	Crematogaster	sp.
Myrmicinae	Cyphomyrmex	minutus
Myrmicinae	Cyphomyrmex	rimosus
Myrmicinae	Pheidole	adrianoi
Myrmicinae	Pheidole	bicarinata
Myrmicinae	Pheidole	bilimeki
Myrmicinae	Pheidole	crassicornis
Myrmicinae	Pheidole	dentata
Myrmicinae	Pheidole	dentigula
Myrmicinae	Pheidole	metallescens
Myrmicinae	Pheidole	morrissii
Myrmicinae	Pheidole	navigans
Myrmicinae	Pheidole	obscurithorax
Myrmicinae	Pheidole	soritis
Myrmicinae	Pheidole	sp.
Myrmicinae	Pheidole	tetra
Myrmicinae	Pheidole	tysoni
Myrmicinae	Pogonomyrmex	badius
Myrmicinae	Pogonomyrmex	badius



Myrmicinae	Solenopsis	invicta
Myrmicinae	Solenopsis	molesta
Myrmicinae	Solenopsis	pergandei
Myrmicinae	Solenopsis	tonsa
Myrmicinae	Solenopsis	xyloni
Myrmicinae	Strumigenys	boneti
Myrmicinae	Strumigenys	epinotalis
Myrmicinae	Strumigenys	louisianae
Myrmicinae	Strumigenys	margaritae
Myrmicinae	Strumigenys	membranifera
Myrmicinae	Strumigenys	sp.
Myrmicinae	Temnothorax	texanus
Myrmicinae	Tetramorium	immigrans
Myrmicinae	Trachymyrmex	septentrionalis
Ponerinae	Hypoponera	inexorata
Ponerinae	Hypoponera	opaciceps
Ponerinae	Hypoponera	opacior
Ponerinae	Odontomachus	brunneus
Ponerinae	Odontomachus	ruginodis

---