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Effects of the Exotic Red Imported Fire Ant (Solenopsis invicta) on the Growth and Survival of the Threatened Hooded Pitcher Plant (Sarracenia minor)

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EFFECTS OF THE EXOTIC RED IMPORTED FIRE ANT (*SOLENOPSIS INVICTA*) ON THE

GROWTH AND SURVIVAL OF THE THREATENED HOODED PITCHER PLANT

(*SARRACENIA MINOR*)

by

Edward Marques

A thesis submitted to the Department of Biology

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CERTIFICATE OF APPROVAL

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ABSTRACT

Plants and insects are some of the most biodiverse groups in the world and are constantly interacting. One unique interaction that has been observed occurs between carnivorous plants and insects; some plant species are capable of capturing and digesting insects for nutrients. Despite preying on these insects, there are cases where such interactions can been viewed as mutualistic. For instance, a nectar reward is produced by the plant to attract insects, and during visitation insects may fall prey to these plants. Additionally, carnivorous myrmecophytic plants may receive an added indirect benefit in the form of reduced herbivory, since ants have the ability to indirectly protect and drive off herbivores from the plant. However, this type of indirect defensive benefit has been rarely observed in carnivorous plants. To determine the nature of the relationship between carnivorous plants and ants, a predator-exclusion experiment was performed *in situ* using a natural population of the hooded pitcher plant, *Sarracenia minor*. The presence of the red imported fire ant, *Solenopsis invicta*, was manipulated in the pitcher plant population to determine if the presence of this non-native ant affects the survival and growth of this carnivorous pitcher plant. From June-November 2014 mean pitcher height and width, number of pitchers, and proportion of pitchers with herbivory present was recorded monthly. Results indicated that pitcher width ($p = .042$) and the number of pitchers ($p = .038$) was significantly lower when the presence of *S. invicta* was reduced. Specifically, the limited presence of *S. invicta* led to a 21% reduction in mean number of pitchers and a 2.2% reduction in mean pitcher width. This indicated that this non-native ant does provide a direct nutritional benefit for the plant. However, the presence of the ant had no effect on pitcher height and the proportion of pitchers with herbivory present. But, when the proportion of pitchers with herbivory present was compared to a previous native ant study, herbivory proportions where

similar or lower when taking the number of ants present into account. This suggests that this non-native ant and native ants equally provide defensive benefits for this native threatened species. Overall, this studied illustrated that carnivorous plants may exhibit similar multiple benefits from a single interaction with a non-native insect that is both prey and provides defense against herbivores.

INTRODUCTION

Plant-Insect Interactions

There are 283,000 described species of plants and 1,013,692 described species of insects, accounting for 78% to 80% of the world's known biodiversity (Costello *et al.*, 2013). Such great biodiversity among plants and insects has led to the evolution of numerous types of interactions between them. Plant-insect interactions are usually grouped (with exceptions) into two broad categories: herbivory and mutualism. Herbivory results when an insect consumes a portion or the entirety of a plant. Because insect herbivory represents a strong selection pressure in many ecosystems, examples of coevolution between plants and insects have been well described (e.g. Ehrlich and Raven, 1964; Hougen-Eitzman and Rausher, 1993; Ramanujan, 2008; Van Zandt and Agrawal, 2013). For instance, some plants have evolved defensive mechanisms such as thorns, spines, and chemicals to deter herbivores (Ehrlich and Raven, 1964; Agrawal *et al.*, 2013; Ramanujan, 2008). In response to these defensive strategies, herbivores have developed different types of resistance to plant defenses. For example, the Monarch butterfly*, Danaus plexippus*, has developed a resistance to milkweed toxin allowing it to consume the generally toxic plant (Dussourd and Eisner, 1987; Holzinger and Wink, 1996): Moreover, *D. plexippus* is also capable of storing the milkweed cardiac glycoside toxin and utilizing it in their own defense against predators.

Conversely, mutualism is defined as the interaction between two organisms where both organisms benefit from one another. One of the most studied mutualistic interaction between plants and insects are pollination complexes. Plants and insects have evolved characteristics and behaviors that enhance this mutualism, such as plants evolving brightly colored flowers to attract

insects and insects altering their behavior to maximize foraging and plant visitations (Hill *et al.*, 1997; Sout *et al.*, 1998; Chittka *et al.*, 1999; Goulson *et al.*, 1997). For example, Houston *et al.* (1993) observed that *Verticordia nitens* and *Verticordia aurea* specifically attract Colletidae bees with their unique, prominently-displayed flowers. As these bees visit flowers they acquire pollen, and inadvertently distribute this pollen to other plants. This exchange of pollen between plants allows fertilization to occur. This insect mediated cross pollination provides plants with a more secure means for successful reproduction than other pollination methods. In exchange for distributing pollen, bees receive food benefits in the form of pollen and nectar when visiting plants.

Another mutualistic interaction between plants and insects is seed dispersal. This type of interaction is readily seen in ants that gather seeds and transport them to their colonies. The placement of seeds in their colonies provides seeds with nutrient –rich substrates and protection from predators. In exchange for seed dispersal, ants receive nutrients in the form of an elaiosome, a detachable food body found on the seed that is composed of lipids, fatty acids, amino acids, sugars, and proteins. This interaction has been observed in North America between many ant species and spring flowering herbaceous plant species (Rico-Gray and Oliveria, 2007).

Mutualisms, such as the one that occurs between the bull's horn *Acacia* tree, *Acacia cornigera* and the acacia ant, *Pseudomyrmex ferruginea*, have been observed to provide multiple benefits to both plant and insect. It has been established that these two species have a mutualistic relationship; Janzen (1966) found that *A. cornigera* provides benefits to *P. ferruginea* in the form of shelter and food resources while *P. ferruginea* provides defenses against potential herbivores. More specifically, *Acacia cornigera* produces large thorns that *P. ferruginea* burrows into and

colonizes. Additionally, *A. cornigera* produces carbohydrate-rich extrafloral nectaries at the base

of its leaves and Beltian bodies at the tip of leaflets that are filled with fats and proteins which

are consumed by *P. ferruginea*. In return, *P. ferruginea* protects *A. cornigera* from herbivores.

Pseudomyrmex ferruginea have been observed to kill insects, attack large vertebrates, and even

cut leafs of encroaching plants. Additionally, *P. ferruginea* are known to clear the base of *A.*

cornigera of herbaceous vegetation, protecting the tree from forest fires and competing plants

(Janzen, 1966).

However, mutualistic interactions between species may have the ability to breakdown if

the cost of the interactions exceed its benefits. This normally occurs when there is an

environmental shift or change. Palmer *et al.* (2008) excluded large mammals for a ten year

period in the African savannah from consuming *Acacia* trees. This resulted in *Acacia* trees

reducing the amount of nectar and thorns produced. In response, ants shifted from a nectar-

dependent mutualist to an antagonistic species that did not depend on plant reward. Similar

mutualistic breakdown have been observed by Janzen (1973) between the plant *Ceropia peltata*

and Azteca ants, *Azteca andreae*. On islands in the Caribbean, *C. peltata* does not produce

glycogen-rich food bodies like *C. peltatas* on the mainland suggesting that the island plants do

not need to attract Azteca ants for their defensive benefits. Janzen (1973) also observed that

herbivory exerted on *C. peltatas* on islands were reduced when compared to that on the

mainland. As a result of reduced herbivory, the mutualistic interaction between *C. peltata* and

Azteca ants were no longer beneficial for the plants on the Caribbean islands.

Carnivorous plants are unique among plants, possessing the ability to capture and consume organisms such as insects to obtain nutrients; yet they are photosynthetic and capable of producing their own carbohydrates (Plummer and Kethley, 1964). These plants trap prey with the use of highly specialized structures composed of modified leaves. Plant carnivory has been theorized to have been independently evolved many times in plants to compensate for living in nitrogen-poor environments (Pietropaolo and Pietropaolo, 1999; Romanowski, 2002). Independent evolution allowed for a diverse set of prey trapping mechanisms. These mechanisms can be grouped into two categories; active and passive traps (Pietropaolo and Pietropaolo, 1999; Romanowski, 2002; Schnell, 2002; Barthlott *et al.*, 2007; McPherson, 2007; Ellison and Gotelli, 2009). A passive trap is defined as a trap that does not require movement to capture prey. The most common passive trap is the pitfall trap, which is simply a trap that insects fall into and become captured. This type of trap will be furthered explained later in the paper. An active trap is defined as a trap that requires movement to capture prey. The most well noted example of this is the Venus fly trap, *Dionea muscipula*. This plant contains hairs in its trapping structures, once these hairs are triggered by the prey it stimulates the plant to close this structure through a complex interaction with tugor pressure, elasticity, and growth to trap the prey. Another example of active traps are those possessed by bladderworts, *Ultricularia* spp. These plants capture small prey like protists and rotifers swimming in water-saturated soil. To accomplish this the plants have small traps that resemble bladders which contain a small opening that is controlled by the triggering of hairs. Once the hairs are triggered the opening is sealed, and ions are pumped out of the bladder as well as water through osmosis. This action creates a vacuum where the prey is sucked into the bladder and becomes trapped and digested.

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However, there has been some debate as to whether these plants actually need to capture prey to fulfill their metabolic need and whether the costs of producing these specialized structures outweigh the profits (Lemmons, 2013). Generally, it is believed that carnivorous plants use both predation and photosynthesis to acquire nutrients and this dual mechanism provides these plants with a competitive advantage over plants in nutrient poor environments that lack these adaptations. Interestingly, another benefit to the hooded pitcher plant, *Sarracenia minor*, has been identified; native ants have been shown to provide defense against herbivores of the pitcher plant (Moon *et al.*, 2012). Defensive benefits associated with insect presence and visitation in addition to acquiring added nutrients may suggest why this characteristic and interaction has been so strongly and independently selected for in nature.

Pitcher Plant: Ecological Importance

Pitcher plants provide numerous beneficial roles in their ecosystem. For instance, they provide nectar resources to a variety of organisms such as ants, beetles, flies to even small vertebrates like tree shrews and Hardwickes wolly bats (Clarke *et al*., 2009; Grafe *et al.,* 2011). Even though the extent to which these organisms rely on pitcher plants for nutrients is unknown, these organisms have been documented to use nectar as a food source.

In addition to providing nutritional resources, some pitcher plants contain communities of organisms and provide a refugia to many micro and macro fauna. These organisms live inside the phytotelmata of pitchers and form inquiline communities. These communities have been thoroughly studied in the pitcher plant, *Sarracenia purpurea*. In *S. purpurea,* inquiline communities are composed of bacteria, mites, midges, protozoa, rotifers, copepods, cladocerans, and dipteran larvae (Fish and Hall, 1978; Bradshaw and Creelman, 1984; Heard, 1994; Kneitel

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and Miller, 2002; Mouquet *et al.*, 2008; terHorst, 2010). Within these communities dipteran larvae are the top predators while rotifers and protozoans feed on bacteria; and the bacteria, mites, and midges feed on detritus. Inquiline communities are beneficial to *S. purpurea* because they provide a source of nutrients and amino acids released by residing organisms (Jones *et al.*, 2009). Therefore, inquiline communities allow for a secondary method for metabolizing captured prey besides the production of digestive enzymes provided by the plant.

Ecology of Sarracenia minor

Sarracenia minor, commonly known as the hooded pitcher plant, is a carnivorous plant native to the southeastern United States. Specifically, the range of *S. minor* includes Georgia, Florida, South Carolina, and North Carolina (USDA, 2012). *Saracenia minor* is a facultative wetland species and as result their natural distribution includes a wide range of environments such as seepage savannahs, bogs, fens, and wet to intermediate pine-barrens (Wunderlin and Hansen, 2008; Hermann, 1995; Meyer *et al.*, 2001; Pietropaolo and Pietropaolo, 1996; Plummer, 1963). *Sarracenia minor* is also a fire-dependent herbaceous perennial; meaning it is aided by the effects of fire to thin densities of competing species. *Sarracenia minor* grows and blooms in the spring and summer seasons and dies back in the autumn and winter seasons (Pietropaolo and Pietropaolo, 1996). It also has the capability to reproduce both asexually and sexually (Barthlott *et al.*, 2007).

Unfortunately, populations of *S. minor* are declining to the extent that the species is listed as a threatened by the state of Florida (Wunderlin and Hansen, 2008; USDA, 2012; Jennings and Roher, 2011). Decreases in *S. minor* populations are primarily due to habitat loss from residential and commercial development (Jennings and Rohr, 2011). Because *S. minor* is a facultative

wetland species, it can tolerate much drier conditions than most other carnivorous plants. As a result of this tolerance, populations of *S. minor* may be found in long leaf pine forests which are a prime locations for development (Herman 1995; Jennings and Rohr, 2011). Other threats to *S. minor* include agriculture, aquaculture, fire suppression, biological resource use, poaching, off-road vehicle traffic, natural systems modifications, invasive and other problematic species, and lastly pollution (Jennings and Rohr, 2011; Chafin, 2008). Therefore, in order to protect *S. minor* populations from further threat, it is critical that we understand the abiotic and biotic factors that hinder or promote the health of *S. minor* populations. This information will allow for the proper establishment of conservation strategies for the threatened hooded pitcher plant.

Trapping Mechanism

Sarracenia minor produces modified leaves that form into small hooded pitchers, relying solely on these passive pitfall trap to capture prey (Herman, 1995). On average, *S. minor* ramets consist of five to twenty pitchers (Moon *et al.*, 2010). These pitchers are primarily green in coloration with the hood occasionally being brightly red colored. This bright coloration acts as a visual cue for insects. In addition, areoles (white-pigmented spots) located on the hood of the pitcher, allow for the passage of light which illuminates the inside of the pitcher. The illumination lures insects into the pitcher to further explore the plant. The entrance of the pitcher is referred to as the lip which is brightly colored and contains extrafloral nectaries. These nectaries produce carbohydrates that attract insects to the entrance of the pitcher. Internal walls of the pitcher contain miniature hairs that point downwards and serve to direct insects towards the base of the pitcher (Lemmons, 2013). Further down in the pitcher, the walls become lined with a waxy cuticle that causes insects to slip and fall to the bottom of the pitcher, which

contains water and enzymes such as amylase, esterase, lipase, phosphatase and protease that are produced by the plant. These plant enzymes along with those produces by resident bacteria help digest insects allowing the plant to absorb vital and limiting nutrients such as phosphorus and nitrogen (Pietropaolo an Pietropaolo, 1996; Romanowski, 2002).

Ants are the most common prey item captured by *S. minor*. For instance, 94% of the biomass found inside *S. minor* pitchers is composed of ant exoskeletons, suggesting that *S. minor* is a myrmecophytic plant (Givnish, 1989; Moon *et al.,* 2010). *Sarracenia. minor* has been documented to capture a wide range of ant species but the most common species is *Solenopsis invicta,* also known as the red imported fire ant (RIFA) (Ellison and Gotelli, 2009; Moon *et al.*, 2010). Despite the association of the hooded pitcher plant and RIFA, the relationship and interaction between *S. minor* and *S. invicta* has been researched very little and is poorly understood. Owing to the relationship that has developed between this threatened native plant and an introduced ant, it is imperative to fully understand the relationship and interaction between these two species. Understanding this relationship could provide valuable information about plant-insect interactions, predator-prey interactions, and conservation techniques for *S. minor*.

Background of Solenopsis invicta

Originally from South America, *S. invicta* is an exotic ant species believed to have been introduced to North America between 1933 and 1945 via a shipping container from Brazil that entered through the county through Mobile, Alabama (Jemal and Hugh-Jones, 1993; Mobley and Redding, 2005; Shattuck and Barnett 2005; Holway *et al.*, 2002). *Solenospsis invicta* has also been introduced to other areas such as Australia, the Caribbean, and Asia (Shattuck and Barnett,

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2005; ISSG 2006). Its range in North America includes Maryland, Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Texas, and Virginia to the west coast including New Mexico, Oklahoma, and California (ISSG, 2006; Williams, 2008; Holway *et al.*, 2002). It's believed that habitat restrictions and its lack of tolerance for cold are the only factors limiting the habitat range of *S. invicta* in North America (ARS, 2003). However, it is likely that *S. invicta's* range will expand over time in temperate regions due to increasing temperatures. Similar distribution expansion is predicted to occur in many other species; for instance, modeling suggests that Monarch butterflies, *D. plexippus* and its host plants *Asclepias spp.* distribution will increase northward due to climate change (Lemoine, 2015). And many plant dominant mountain top species in Southern California have already expanded their range up mountains by approximately 65 m in a 30-year period (Kelly and Goulden, 2008).

Typical of aculeate hymenopterans, *S. invicta* possess a modified ovipositor (stinger) that the ant uses offensively and defensively. When using its stinger, female ants may inject an alkaloid venom into organisms. The venom is toxic and can be delivered via multiple stings that can kill small animals such as lizards. For humans the venom is painful and causes white pustules to appear the following day (Cohen, 1992). The name fire ant is a reference to the pain induced by the venom which has been compared to an intense burning sensation.

Like many introduced species, *S. invicta* is considered a pest. As a generalist, it consume invertebrates, small vertebrates, carrion, and sugary substances (honey dew and nectar) (USDA, 1993; Vinson and Sorenson, 1986; Mount, 1981). However, the key feature that makes these ants such a nuisance and dangerous especially in disturbed habitats is their aggressive behavior and ability to rapidly form new colonies (Langkidle 2009; Adams and Balas, 1999). *Solenopsis*

invicta is extremely hostile and may attack any foreign organisms they encounter. Their aggressive behavior is so formidable that it has been hypothesized to have selected for behavioral (avoidance of *S. invicta*) and morphological adaptations (longer hind limbs) in Eastern fence lizards, *Sceloporus undulates*, since its introduction 70 years ago (Langkidle, 2009). These rapid evolutionary adaptation in lizards suggests that *S. invicta* is a primary source of mortality in Eastern fence lizards.

However, the aggressive behavior that makes *S. invicta* such a threat too many species may benefit *S. minor*. It's been previously noted that the presence and visitation of native ant species benefits *S. minor* in two distinct manners. First, an increase in ant presence and visitation led to direct nutritional benefits for *S. minor*. Second, depredation by native ants significantly reduced herbivory of *S. minor* from the pitcher-mining moth, *Exyra semicrocea* (Moon *et al.*, 2008). If these less aggressive native ants have such a significant effect on deterring herbivores from *S.minor*, then *S. invicta*, which is more bellicose than native ants, may reduce pitcher plant herbivory more than endemic species. Thus, this much-maligned invasive species may actually aid in maintaining healthy pitcher plant populations

Interactions between Native and Non-native Species

The benefits of non-native organisms to their invaded communities are poorly understood, but examples have been reported (Keller *et al.* 2007; Rogalski and Skelly, 2012; Bulleria *et al.*, 2008; Pec and Carlton, 2014). For instance, Pec and Carlton (2014) showed that a native herbaceous tree, *Cryptantha muricata,* in Southern California benefited in survival, growth, and reproduction from the presence of non-native grasses (*Avena barbata, Bromus diandrus, B. madritensis* ssp. *rubens, B. tectorum, Ehrharta calycina* and *Festuca myuros)*. These grasses

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benefited this herbaceous tree species by inhibiting the establishment and growth of competing woody tree species. Another study conducted by Glefitsch and Carlo (2011) illustrated a strong positive correlation between the presence of non-native honeysuckles, *Lonicera*, and the establishment of native frugivore bird communities such as *Dumetella carolinensis* and *Turdus migratorius*. The strong correlation suggests that this non-native berry is the primary source of nutrients for these bird communities. Therefore, similar beneficial interactions is plausible between the native *S. minor* and non-native *S. invicta.*

Objectives

The main goal of my study was to characterize the direct and indirect effects of *S. invicta* on both the survival and performance of *S. minor*. An expected direct effect of higher nutrient levels for *S. minor* provided by *S. invicta* should be evident in plants with consistent interaction with *S. invicta* than plants deprived of this interaction, since ants are the most common prey item available for this plant (Moon *et al.* 2010; Ellison and Gotelli, 2009)**.** In addition, a proposed decrease in herbivory and pitcher mortality are both forms of indirect effects that are induced by the presence and behavior of *S. invicta*. High aggression may play a role in deterring insect herbivores from visiting the plant which in turn may increase pitcher plant survival and its ability to capture prey.

METHODS

Study site

This study took place on a 65 x 20 m stretch of cleared pine barren located along a Jacksonville Electric Authority (JEA) power line corridor near McGirt's Creek Park in

Jacksonville, FL (N: 30°13.432'; W: 081°46.965') (Lemmons, 2013) from June-November 2014 (Figs. 1 and 2). This site was selected based on two key features; it is semi-protected from the public and contains healthy populations of both *S. minor* and *S. invicta*. Because these two species thrive in open, periodically disturbed habitats, biannual mowing at this site acts as a source of occasional disturbance which *S. invicta* prefers and may substitute as a fire disturbance known to benefit *S. minor* (Herman, 1995; Stuble, 2011). This source of disruption likely limits the colonization and presence of native ants that prefer pristine and less distributed area and may compete poorly with *S. invicta*.

Experimental Field Design

To examine the effects of *S. invicta* on the mortality and performance of *S. minor*, a presence-exclusion experimental approach was used in the study. Fifteen 3x3 meter plots were established within the populations of *S.minor* ramets and *S. inivicta* colonies. Three treatments were used in this study excluded, present, and open treatments. Each treatment group was replicated in five plots, with at least two *S. minor* ramets present in each to avoid a plot sample size of one. *S. minor* ramets were selected for each treatment based on their proximity to an initial *S. invicta* colony. The ramets with colonies closest to them were selected for the present and open (control) treatment. The open treatment had an n = 27, the present had an n = 18, and the excluded treatment had an n = 50.

The manipulative treatment in this study was the exclusion of *S. invicta* from plots containing *S. minor* (excluded treatment). In order to ensure that *S. invicta* ants were completely excluded from field plots, numerous precautions were taken. First, a drift fence composed of 25 cm high aluminum flashing and 45 cm wooden pine stakes was constructed around the exclusion

plots. The drift fence was placed flush against the ground to prevent holes between the ground and the drift fence. Secondly, Tangle Trap™ (115 19 Dallas RD, Victoria, BC V8V 5A6, Cannada), a sticky petroleum-based agricultural product was used to create a barrier along the very top edge of the drift fence to prevent *S. invicta* ants from entering the plot. Specifically, Tangle Trap™ was applied as a thin layer so that only smaller insects like *S. invicta* were excluded but not larger insects. Tangle Trap™ was reapplied as needed to the drift fence throughout the study. Lastly, four tablespoons of AMDRO™ (2030 Powers Ferry Road, Suite 370, Atlanta, GA 30339) a fire ant pesticide, was applied to field plots on a monthly basis as directed by the manufacturer's instructions. These exclusion practices did not exclude *Exyra semicrocea* because of its ability to fly over the barriers.

Two control treatments were used in this study. Although both treatments included the presence of *S. invicta*, one treatment specifically tested the effects of caging alone. To test for any caging effects, a drift fence was placed around five plots (present treatment) while the five remaining plots were completely open to the environment and did not have drift fencing bordering the plots (open treatment).

Once all the plots were constructed individual *S. minor* ramets were marked using wire flags and given a unique identification number for monitoring purposes. Individual *S. minor* ramets were measured once a month from June-November 2014. These measurements included number of pitchers, average pitcher height (mm) and width (mm), and the number pitchers with herbivory present. Average mature pitcher height and width were taken by measuring three mature pitchers and then averaging the height and width of all three. If three mature pitchers were not present, all mature pitchers were measured and averaged. Pitcher height was measured

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to the nearest millimeter from the ground to the apex of the hood using a plastic a ruler to the

nearest millimeter. Pitcher width was measured to the nearest .01 mm with the use of digital

calipers. Herbivory was recorded as present if any holes or brown discoloration were present on

the pitchers. The brown discoloration and holes on pitchers are caused by *E. semicrocea*

caterpillars which consume pitchers from the inside (Moon *et* al., 2008).

Solenopsis invicta Visitation

Ant visitation per plot was measured in order to test whether the exclusion treatments were

successful. Pitfall traps composed of a petri dish and a 1:1 mixture of radiator fluid and maple

syrup were placed in the middle of all the plots for five days. After the fifth day, the traps were

collected and observed in the lab under a magnifying glass. The number of *S. invicta* captured in

the traps were recorded. This sampling method was repeated four times throughout the study. A

second monitoring method used in this study involved selecting one *S. minor* ramet per plot if

sample size permitted (n>2) with the use of a random number generator. The selected *S. minor*

ramet measurements (the number of pitchers, average pitcher height and width, and the number

pitchers with herbivory present) were not included in the data (to prevent pseudoreplication) but

were still measured normally throughout the study to ensure that the *S. minor* ramet sampled was

not an outlier. After three months, the two tallest pitchers of the selected *S.minor* ramets were

collected. This was performed by cutting the pitchers as close as possible to the ground. The

pitchers were then brought back to the laboratory and cut open from the apex to the bottom with

a razor blade. Pitcher contents were placed on a weigh boat and observed under a dissecting

microscope for *S. invicta* head capsules. Only head capsules were counted and recorded to

prevent recounting of the same ants that may have been broken apart due to digestive enzymes

inside of the pitchers. After the field study was concluded (six months), this process was

repeated using the previously sampled *S. minor* ramets. Plots previously not sampled due to

small sample (n<2) size were also sampled.

Solenopsis Invicta also has distinct characteristics that enable them to quickly be

differentiated from native ant species. Specifically, *S. invicta* can be identified by its two-

segmented pedicel (the region that connects the thorax and abdomen.), most similar native ants

possess one. Another distinguishable characteristic is the genticulated ten-segmented antenna

that ends in a two-segmented club (Hedges, 1998; Hedges, 1997). For instance the native

Acrobat Ant, *Crematogaster ashmeadi,* which was the most abundantly captured ant in Moon *et*

al. (2010), also contains a two-segmented petiole but the first segment is wider than the second.

It also contains a genticulated eleven-segmented antenna that ends in a three-segmented club, a

pair of spines on a propodeum, and a ventrally convex gaster (Vail *et al.,* 1994). The native fire

ant, *Solenopsis geminate*, is very similar in appearance to *S. invicta,* the only main differences is

that this species contains a small "tooth" which a central clypeal hair emerges and the workers

are large-headed (Vail *et al.* 1994; Clouse, 2007). All of these unique characteristics were used to

identify ant species. In addition, the entire study site was examined monthly for ant mounds and

the species for each mound was identified (All mounds observed belonged to *S. invicta*).

Prey diversity

The number of unique insects visiting the plots each week was also measured. This was

accomplished by placing sticky traps composed of yellow neon painted index cards wrapped in

transparency film and coated with Tangle Trap™ in the middle of the plots. Sticky traps were

left out at the beginning of each week and collected at the end of the week throughout the

entirety of the field study. Once collected, the sticky traps were observed under a dissecting microscope and the number of each unique species was recorded. The single highest recorded number of unique species for each plot was used to compare each treatment in the statistical analysis.

Statistical Analyses of Treatment

To compare ant visitation, ant capture, and prey diversity between treatments a one-way ANOVAs and a Tukey's HSD post hoc test was used when significant main effects were found. To compare number of pitchers, average pitcher height and width, and proportion of pitchers with herbivory present four repeated-measures ANOVAs was used. Furthermore, the values obtained with the repeated-measures ANOVAs did not meet the assumption of sphericity. Therefore, the Greenhouse-Geisser procedure was used to estimate epsilon and correct the degrees of freedom. The Greenhouse-Geisser correction was used instead of the Huynh-Feldt correction because it is known to be the more conservative correction.

RESULTS

The mean number of ants collected using pitfall traps, was not significantly different between treatments ($F_{2, 14} = 1.35$, $p = .297$) suggesting similar visitation rates between treatment plots (Fig. 3). However, the number of ants found inside the pitchers showed a highly significant difference among treatments, with *S. invicta* presence being reduced by 85% ($F_{2, 14} = 8.168$, p =.006) (Fig. 4).

A repeated measures ANOVA indicated that the presence of *S. invicta* had significant effects on the number of pitchers ($F_{6.03} = 2.26$, p = .038) and pitcher width ($F_{6.13} = 2.19$, p =.042)

(Fig. 5 and 7). Specifically, the limited presence of *S. invicta* led to a 21% reduction in mean number of pitchers and a 2.2% reduction in average pitcher width. Furthermore, prey diversity was significantly different among treatment ($F_2 = 5.49$, p = .020) (Fig. 9). The limited presence of *S. invicta* resulted in a 20% reduction in prey diversity. However, pitcher height ($F_{6.64} = .672$, p = .688) and the proportion of pitchers with herbivory present ($F_{5.11} = 1.59$, p = .165) showed no significant differences between treatments even though an increased amount of *S. invicta* lowered herbivory by 9% (Fig. 6 and 8).

Additionally, time had a significant effect on proportion of pitcher with herbivory present ($F_{2.55} = 8.26$, p = <.001), number of pitchers produced ($F_{3.01} = 14.59$, p = <.001), and pitcher width ($F_{3.07} = 6.930$, p = <.001). However, time was trending towards having a significant effect on pitcher height ($F_{3.32} = 2.116$, and p = .092). As a result, pitcher height, pitcher width, and number of pitchers exhibited a parabolic trend over time, all having an increase and reaching a high in September before declining later on. The proportion of herbivory present on pitchers displayed an increasing trend over time.

DISCUSSION

Ant capture rates (the number of ants found inside the pitchers) was significantly different between all treatments. Although the exclusion treatment did not completely prevent *S. invicta* from being captured, the results indicate that the treatment significantly reduced the number of ants captured by *S. minor* when compared to the control plots. Such a reduction of *S. invicta* ants could potentially limit nutrient absorption in *S. minor* leading to poor growth and decreased pitcher production.

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Even though ant capture was significantly different between all treatments, ant visitation (the number of ants captured by pitfall traps) was not significantly different between treatments, which was not consistent with predictions that *S. invicta* would be excluded or significantly reduced in the exclusion treatment. Such contrasting results could have arisen from a small sample size (n= 4) in regards to the ant visitation data or could have been caused by preference for *S. minor* nectar. It is possible that *S. invicta* workers favored *S. minor* nectar over the 1:1 mixture of maple syrup and radiator fluid that was placed inside pitfall traps. This preference may have led ants to visit plants more frequently causing an increase in ant capture by *S. minor*. As a result of these potential explanations, ant visitation results were not heavily used as an indicative measure of the presence of *S. invicta*. Instead, results from the ant capture observations were used as a reliable measure for ant presence. Thus, using this measure, the methods used to reduce *S. invicta* ants in specified treatments worked effectively in this study.

Number of pitchers and pitcher width was significantly lower when *S. invicta* was limited from plots, indicating that these plant were lacking nutrition which could potentially be related to the limiting numbers of *S. invicta* present. However, mean pitcher height was not significantly different among treatments, indicating that pitcher height is not affected by the presence of *S. invicta*. Although previous studies on *S. minor* show that average pitcher width and pitcher height tend to exhibit similar growth patterns (Moon *et al.*, 2010). Differences between pitcher width and height in this study may be due to disparities in sensitivity to fluctuations of available nutrients.

In addition, it has been observed in a closely related species, *Sarracenia purpurea*, that pitcher plants can store nitrogen in tissues and use this stored nutrient the following growing season (Butler and Ellison, 2007). If *S. minor* has a similar ability to store nitrogen, it is probable

that any effects that the treatments may have had on the plants may have been somewhat negated by previously stored nutrients leading to the observed outcome on pitcher height. Allowing this study to continue over multiple growing seasons might lead to more direct results regarding pitcher height and tease out any effects due to nutrient storing. Overall, the results are consistent with expectations that the presence of *S. invicta* will lead to direct nutritional benefit for *S. minor*.

These findings are consistent with previous studies investigating *S. minor* and ant interactions. Moon *et al.* (2010) observed nutritional benefits such as increased average pitcher height, pitcher width, and number of pitchers with regards to higher native ant visitation and ant capture. However, the duration of the Moon *et al.* (2010) study was considerably longer compared to this study, 13 months to 6 months, respectively. This extended amount of time may have played a role in the observed changes in pitcher height. Furthermore, in similar prey limiting experiments with *Sarracenia purpurea*, the addition of prey did not lead to direct nutritional benefits (Chapin and Pastor, 1995; Wakefield *et al.*, 2005). Therefore, it seems that nutrient limitations can affect different species of carnivorous plants even those belonging in the same genus very differently.

The proportion of pitchers with herbivory present was not significantly different among treatments, which indicates that all *S. minor* ramets regardless of being exposed to normal or reduced presence of *S. invicta* were subjected to equal amounts of herbivory. These results differ from Moon *et al.* (2010) who found that an increase in native ant visitation led to a decrease in herbivory in *S. minor*. This could potentially signify that *S. invicta* does not deter herbivores from consuming *S. minor* as effectively as native ants. Another possible explanation is that only a few *S. invicta* ants are necessary to deter herbivores from consuming *S. minor* and that increase

in the abundance of *S. invicta* does not necessarily correlate with a reduce amount of herbivory.

When examining native ant visitation and its effect on herbivory in *S. minor*, Moon *et al.* (2010)

found that the average proportion of herbivory when roughly 45 ants were captured was

approximately 67%. However, the average proportion of herbivory under limited *S. invicta*

visitation (22 ants captured) was 59%, suggesting that the presence of *S. invicta* can reduce the

amount of herbivory more effectively than a similar number of native ants. Since, *S. invicta*

workers are much more aggressive than native ant workers, it is possible that such formidable

aggression plays a large role in deterring herbivores from consuming *S. minor* plants at low ant

presence.

However, as the number of native ants increases (~90 ants captured) the proportion of

herbivory decreases to around 46% (Moon *et al.*, 2010), compared to typical numbers of *S.*

invicta present (~140 ants captured) the proportion of herbivory present decreases to 50%. Thus,

the magnitude of deterring herbivores is nearly equivalent, which supports the idea that an

increase in *S. invicta* does not decrease herbivory significantly and that an herbivory threshold is

reached. It may be that *S. invicta* reaches this herbivory threshold more quickly with fewer ants

than native ants due to their highly aggressive behavior. One also has to take into account that

these studies were conducted in separate years and in different habitat types, so differences in

weather and herbivore densities could also be affecting these proportions. Nonetheless, it does

seem that *S. invicta* is able to deter herbivores from consuming *S. minor* and thus offers an

indirect protection for the plant, regardless of an increase in the number of *S. invicta*. This

defensive benefit exerted by *S. invicta* is consistent with other mutualistic plant-insect

interactions. Kuptor (1984) observed that some ant species deterred herbivores more effectively

than others, but herbivory overall on the plants was significantly less when ants were present.

Additionally, prey diversity was significantly lower in the excluded treatment than the control treatment. This may suggest that the presence of *S. invicta* increases prey diversity in *S. minor's* habitat. This may be accomplished by *S. invicta* aggressive behavior deterring predators of these species from hunting near their colonies and food supplies. This contradicts a previous study that observed *S. invicta* lowering all insect biodiversity regardless of the insect being a predator or herbivore (Eubanks, 2001).

Overall, these results suggest that the presence of the invasive *S. invicta* is beneficial to the threatened native *S. minor*. This is one of the first robust examples of *S. invicta* directly and indirectly benefiting a native species. Although a previous study noted that *S. invicta* does limit agricultural pest of cotton and soybean plants, it also limits the biological controls of these pests as well (Eubanks, 2001). This a crucial outcome because most research conducted on *S. invicta* focuses on the negative impacts that this organism has had in introduced ecosystems. However, recent research has shown that these impacts may have been overstated. Morrison and Porter (2003) showed positive correlations between *S. invicta* densities and species richness for non-*S. invicta* ants and non-ant arthropods, suggesting that these sampled communities are more resistant to *S. invicta* invasion that previously thought. Similar findings were observed by King and Tschinkel (2006), when the presence of the red imported fire ant colonies were limited in pastures, there was no change in co-occurring ant species. This may indicate that *S. invicta* is not a superior competitor to native ants and that other factors such as disturbances and recruitment limitations may be the limiting factor for native species in specific habitats. Conservationists preserving *S. minor* should take these studies into account as well as the lack of a biological control for *S. invicta*, and assess whether removing *S. invicta* from their conservation areas will

in fact benefit communities and if this benefit outweighs the positive effects *S. invicta* will have on the threatened *S. minor* populations.

This study provides an example of a mutualistic plant-insect interaction between *S. minor* and *S. invicta* and is also an example of a New World pitcher plant that is indirectly benefited by a New World non-native ant species. The only other example has been observed by Moon *et al.* (2010) with *S. minor* and native ants. However, another example of a beneficial relationship has been described in Borneo between *Nepenthes bicalcarata* and *Camponotus schmitzi*. These ants colonize and occupy *N. bicalcarata* tendrils and in return deter weevils from consuming the plant (Clarke and Kitching, 1995; Merbach *et al*., 2007). With growing examples of defensive benefits being observed between carnivorous plants and insects, this interaction may function as a crucial benefit for the selection of these unique carnivory structures. Rutter and Rausher (2004) noted that extrafloral nectaries are produced at a great expense to plants, and thus should only be observed in plants that can offset this cost. With the low capture rates being observed by pitcher plants, only .37% of prey is captured when visiting the plant, thus carnivory alone is questioned to fulfill these offsetting requirements (Newell and Nastase, 1998). However, when combining the added benefit of defense against herbivores and extra nutrients these benefits may overshadow the steep costs of producing extrafloral nectaries and pitchers.

However, much is still unknown about the relationship between *S. minor* and native and introduced ants. Further investigation should primarily focus on indirect defensive benefits of native ants and introduced ants. Conducting a study that simultaneously observes both ant types and its effects on *S. minor* through multiple growing seasons could help resolve which ant species significantly prevents herbivory. Also, by adding a treatment that excludes ants but not herbivores may help illustrate the magnitude of herbivory deterrence performed by these ants.

Another area that should to be furthered examined to strengthen conservation efforts of *S. minor* is germination. It has been observed that germination time of *S. minor* seeds is prolonged, potentially reaching five years. Understanding what factors influence this slow germination process may lead to novel ways for conservationists to speed up the process and quickly increase *S. minor* populations in the future.
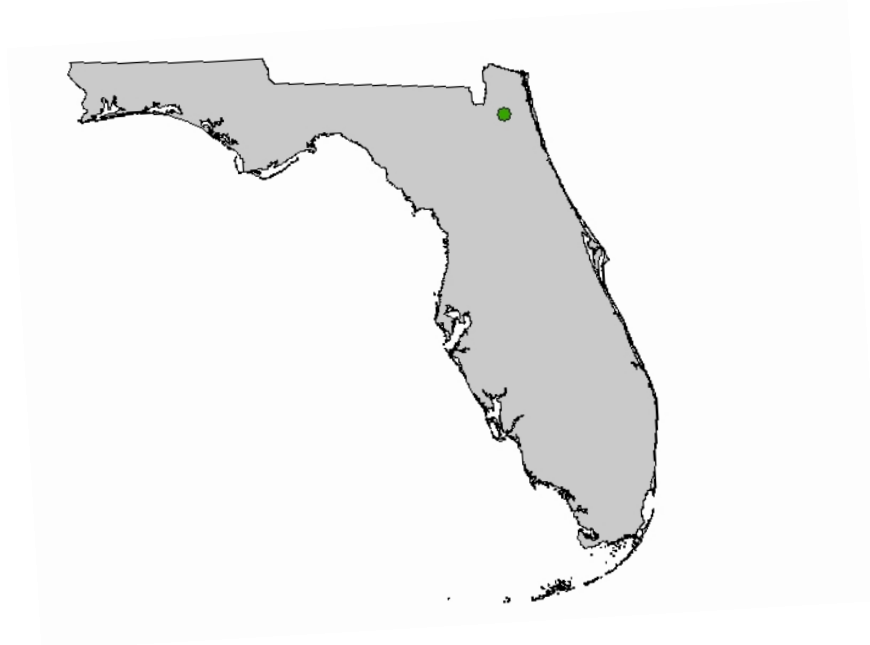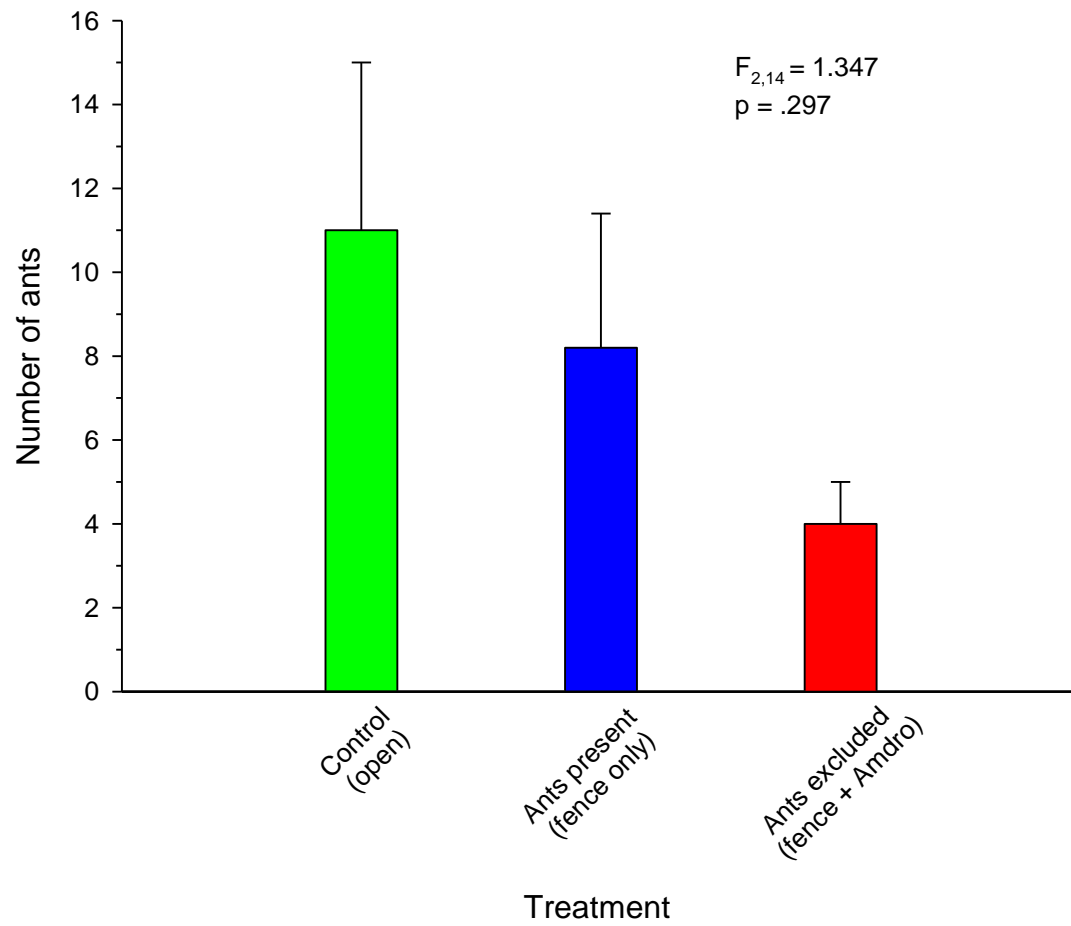
Figure 1: Map of Florida where a *Sarracenia minor* population was used for this study.
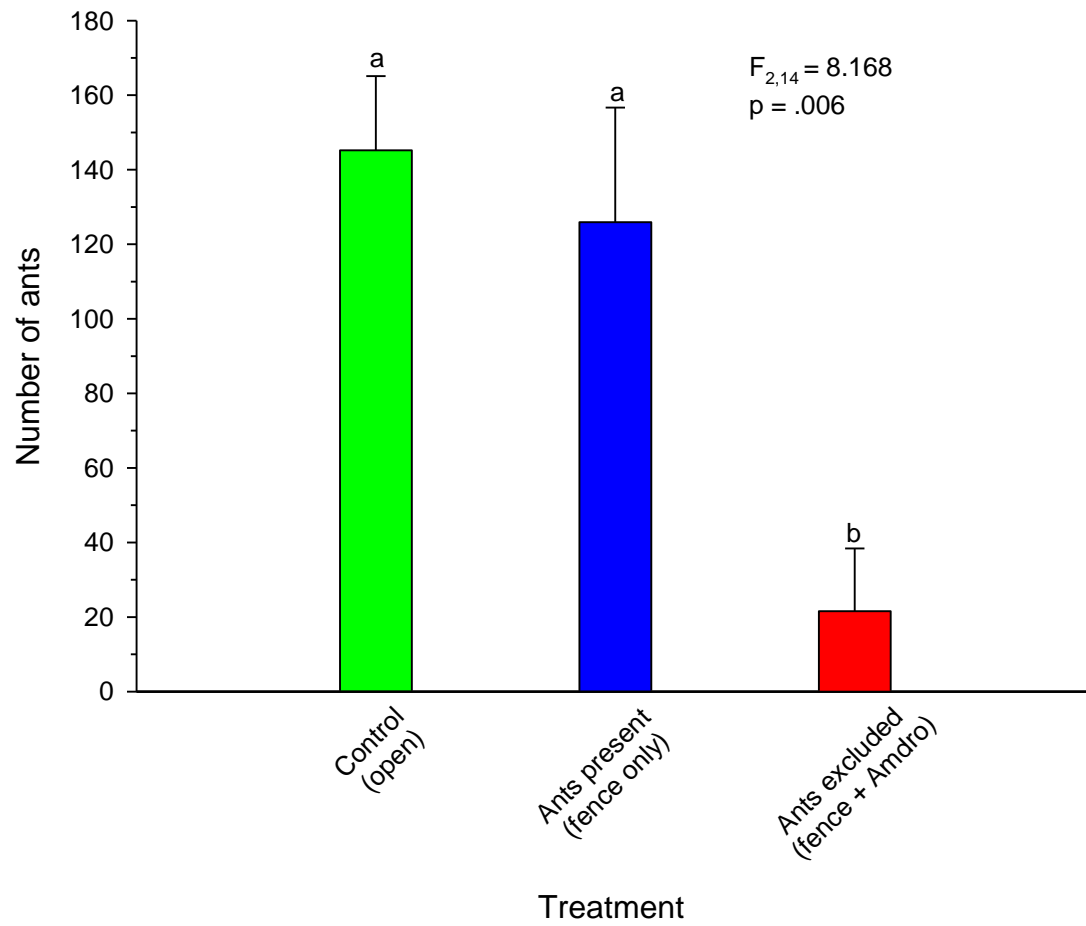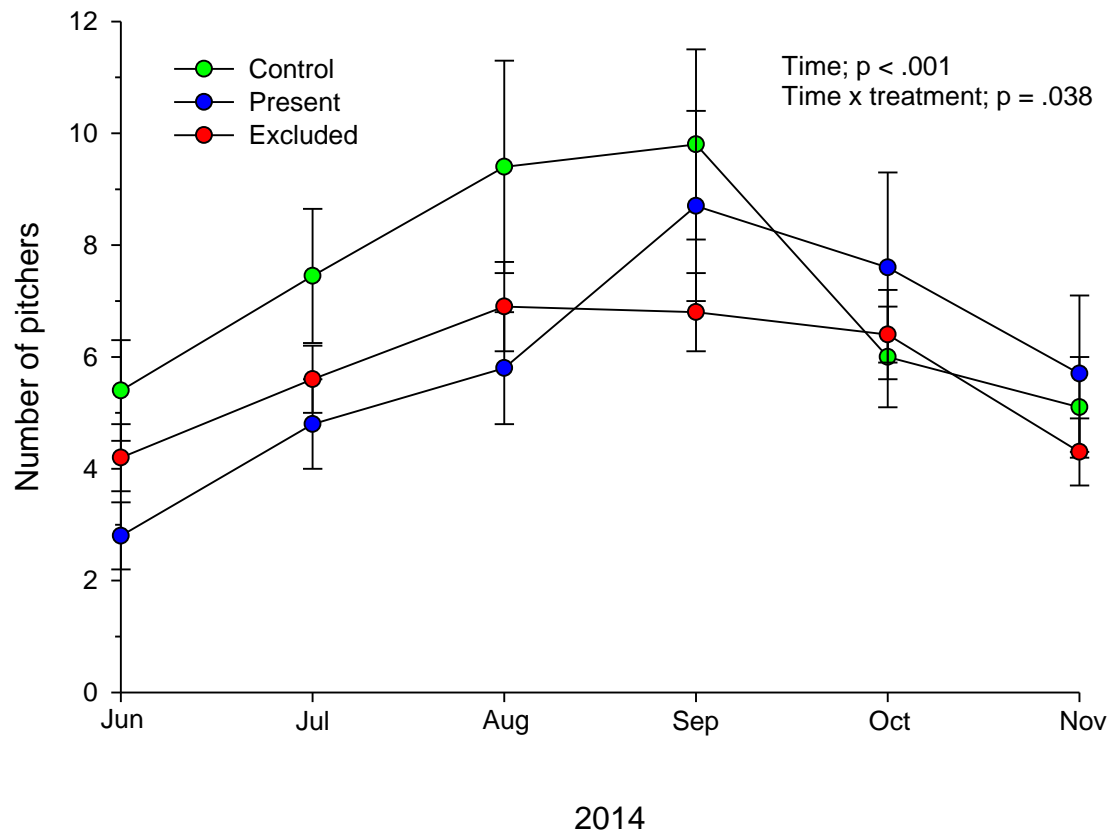
Figure 2: Aerial photo of the power line corridor where the study site was located in. The box highlights the border of the study site.
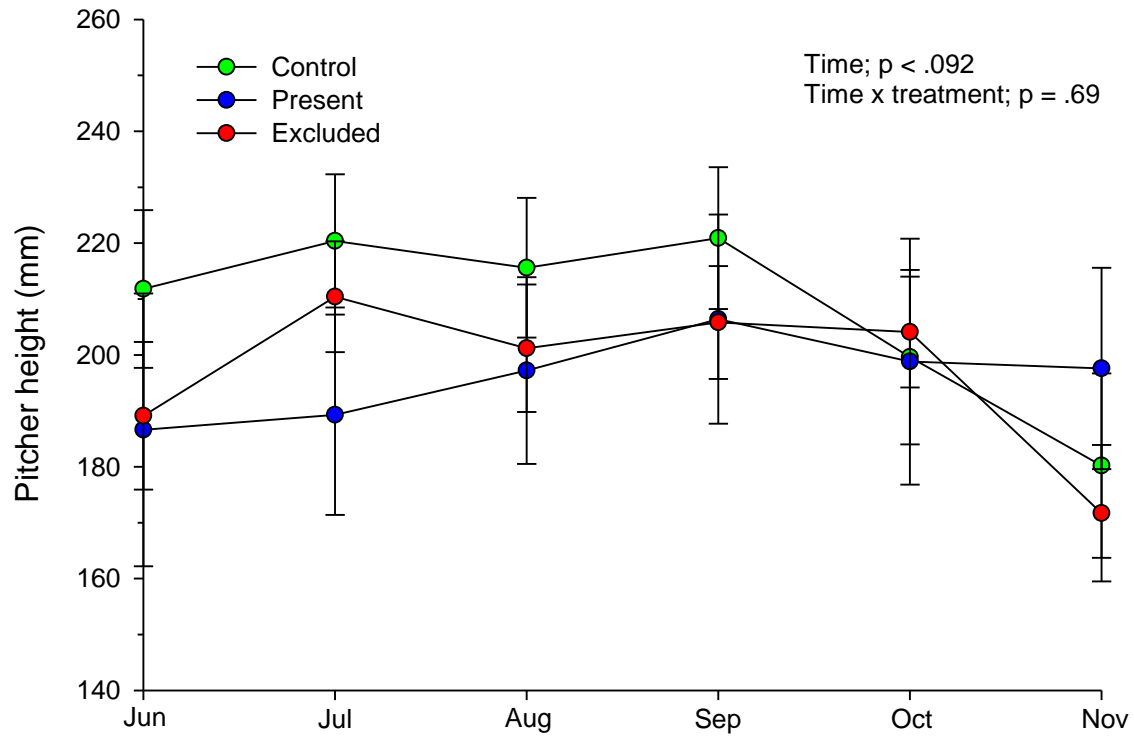
Figure 3: The mean (± SD) number of ants visiting each treatment.

Figure 4: The mean (± SD) number of ants captured per pitcher for each treatment.
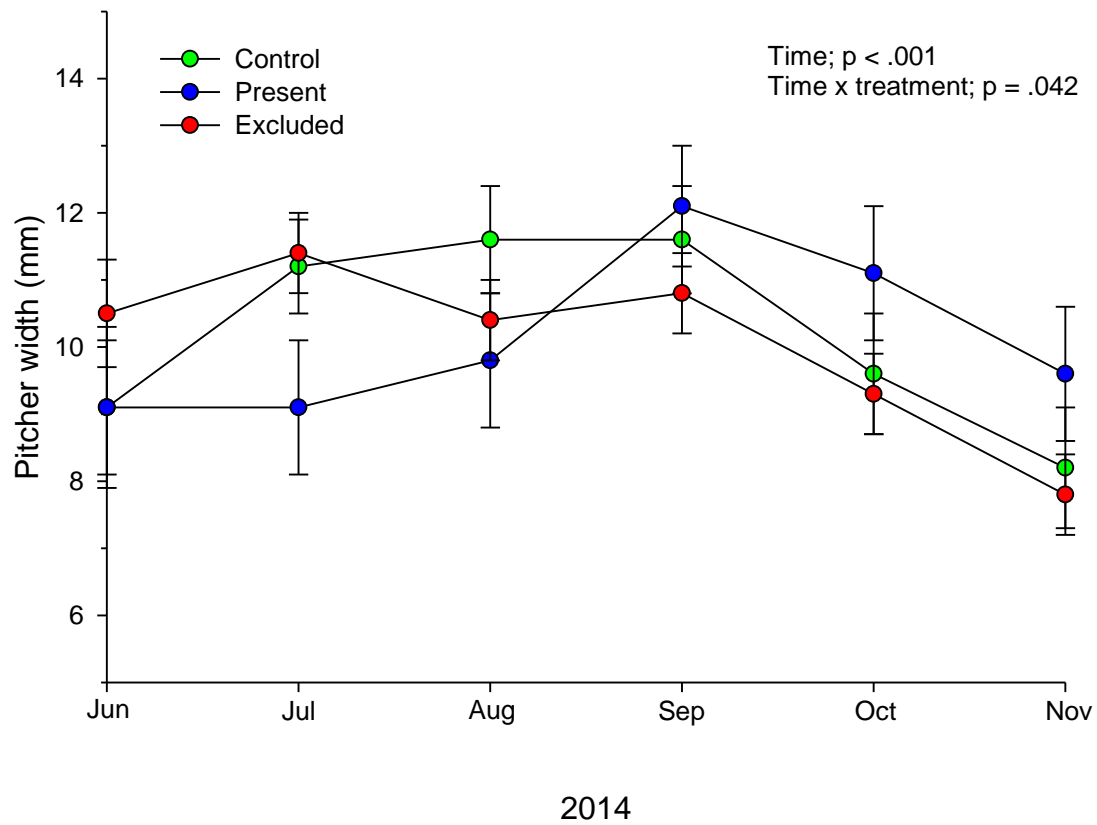
Figure 5: The mean (± SEM) number pitchers for each treatment throughout time.
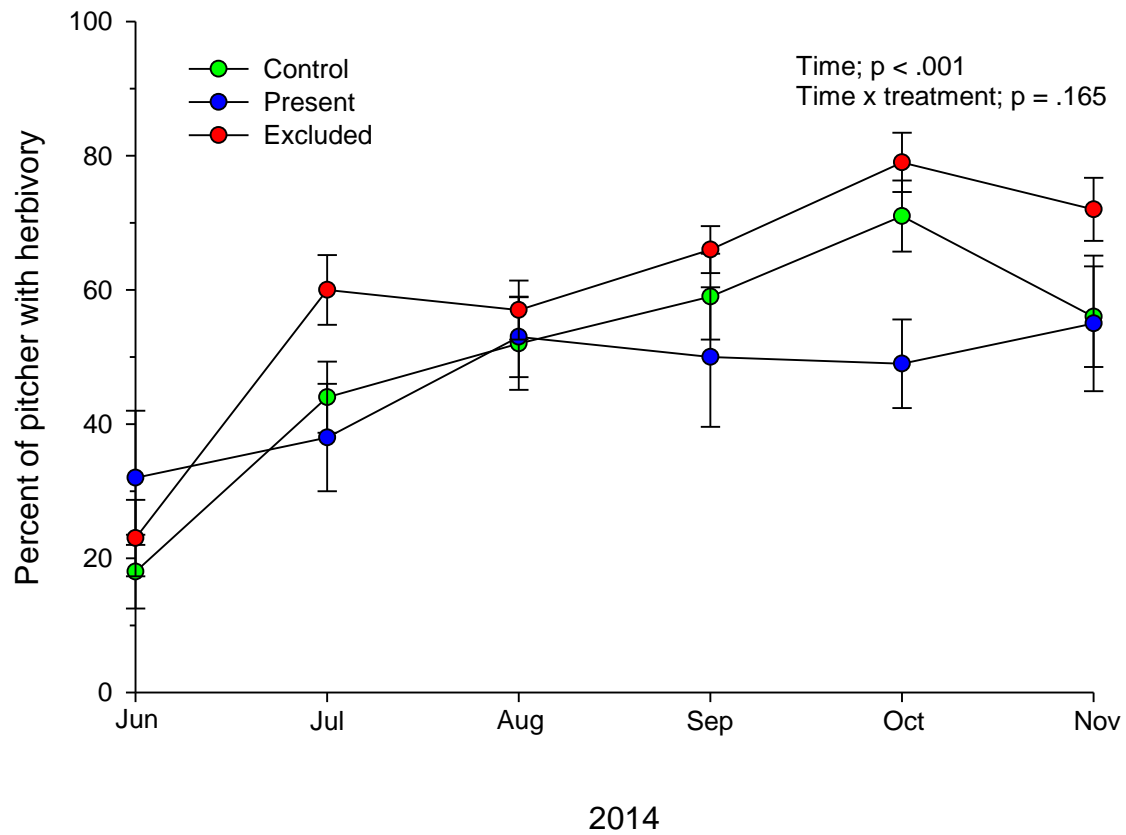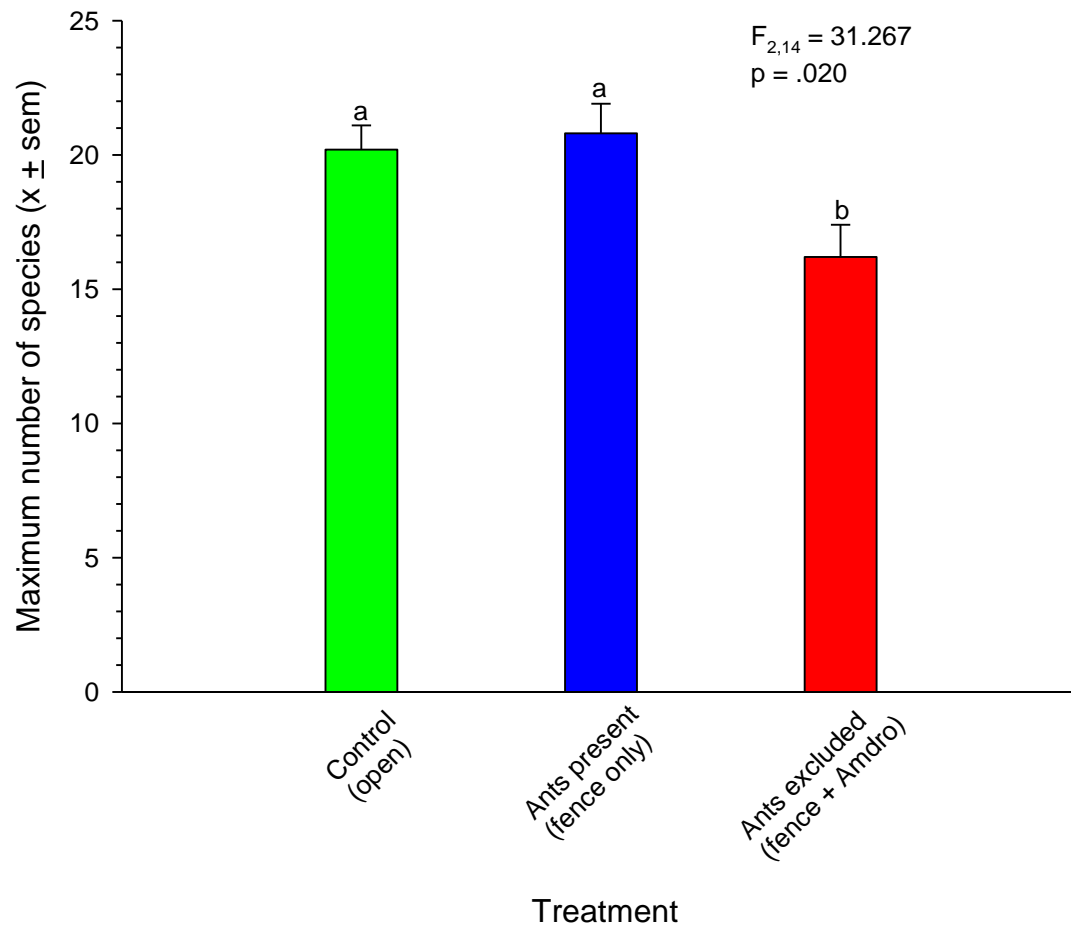
Figure 6: Mean (± SEM) pitcher height in mm for each treatment throughout time.

Figure 7: Mean (+ SEM) pitcher width in mm for each treatment throughout time.

Figure 8: The mean (± SEM) percent of pitchers with herbivory present for each treatment throughout time.

Figure 9: The mean (± SEM) amount of unique species observed in each treatment.

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EDWARD MARQUES

EDUCATION

University of North Florida, Jacksonville, FL
M.S. in Biological Science   **2015**

Florida State University, Tallahassee, FL
B.S. in Biological Science   **2012**

AWARDS

Coastal Biology Travel Grant, University of North Florida   **2015**
Graduate Grant, University of North Florida   **2014 – 2015**
Freshmen Incentive Scholarship, Florida State University   **2008 – 2012**
Florida Academic Scholars Scholarship, FL. Dept. of Education   **2008 – 2012**
James R. Hoffa Memorial Scholarship, Int. Brotherhood of Teamsters **2008**
Rotary Foundation Scholarship, Rotary Foundation Inc.   **2008**

RESEARCH EXPERIENCE

University of North Florida, Jacksonville, FL
Graduate Student for Dr. Tony Rossi   **2013 – Present**
Conducting a manipulated field study focused on the beneficial
effects of the exotic *S. Invicta* on the threatened *S. minor*.

Florida State University, Tallahassee, FL
Laboratory Technician for Dr. David Houle   **2012 – 2013**
Helped investigate the evolutionary morphology of *D.
melanogaster* by specifically studying the allometry and plasticity
of the fruit fly wing.
Supervised undergraduate research projects.

Florida State University, Tallahassee, FL
Laboratory Technician for Dr. Nora Underwood   **2012**
Extracted Microsatellite DNA from *Solanum* samples to determine
which samples underwent clonal replication.

Florida State University, Tallahassee, FL
Laboratory Volunteer for Dr. Alice Winn   **2011 – 2012**
Conducted a greenhouse experiment to determine the effects of
soil type on shoot and root growth on different populations of
Pityopsis.

Florida State University, Tallahassee, FL
Field Volunteer for Erik Peterson   **2011**
Transplanted *Pityopsis* seedlings from a greenhouse to field sites.

Florida State University, Tallahassee, FL
Laboratory Volunteer for Dr. Christopher Oakley   **2010 – 2011**
Helped with data collection and observations of plant matter to
determine phenotype variation in the endangered *H. Cumulicola*.

TEACHING EXPERIENCE
University of North Florida, Jacksonville, FL
Graduate Teaching Assistant   **2014**
General Biology I Laboratory

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General Biology II Laboratory

MANUSCRIPTS IN PREPARATION & PRESENTATIONS
Marques, E. and Rossi, A. "The effects of the Red Imported Fire Ant *(S. Invicta)* on the growth
and survival of threatened Hooded Pitcher Plant (*S. minor*). Manuscript in preparation.

Marques, E. and Rossi, A. "The effects of the Red Imported Fire Ant *(S. Invicta)* on the growth
and survival of threatened Hooded Pitcher Plant (*S. minor*). Poster presentation at the 2015
meeting for Society for Integrative and Comparative Biology.