ANTS IN YOUR PLANTS: FLORAL RESOURCE DIVERSITY ON ORGANIC FARMS INCREASES INVASIVE FIRE ANTS RATHER THAN NON-INVASIVE PREDATORS

by

AMY SPARER

(Under the Direction of Carmen Blubaugh and Kris Braman)

ABSTRACT

Increasing plant diversity in agroecosystems strengthens pest suppression yet predicting which non-crop diversity type best supports biocontrol remains challenging. Farmers often supplement non-crop diversity with managed flowers or by allowing weed persistence both of which may bolster natural enemy communities that provide biocontrol. Concurrently, natural enemy balance and biocontrol effectiveness may be compromised by dominant invasive predators co-benefitting from non-crop diversity. We examined whether flowers or weeds had stronger balancing effects on insect predator communities by surveying plants and insects on zucchini at 37 organic farms. Neither flowers nor weeds affected natural enemy evenness. Invasive red imported fire ants (*Solenopsis invicta* Buren) were the single significant and negative predictor of non-invasive insect predator evenness. Fire ant activity increased with floral resource availability; neither fire ants nor non-invasive predators predicted prey removal, suggesting floral diversity may not reliably predict biocontrol when invasive predators interfere with non-invasive predator community structure and function.

INDEX WORDS: *evenness, plant diversity, biological control, floral resources, natural enemies, red imported fire ant*

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The University of Georgia
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DEDICATION

For Kim Van Fleet and Dr. Jason Smith for introducing me to the joys and sorrows of field work and Entomology. For my parents, Susan Bielanski Sparer and Cary Sparer, who encouraged me from a young age to be kind to small creatures, admire spider webs, and look under rocks for creepy-crawly things. For Alex, with love, who looks under rocks by my side and supports me unwaveringly.

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CHAPTER 1

RELATIVE ATTRACTIVENESS OF FLORAL TRAITS TO INSECT NATURAL ENEMIES

Ecosystems services are beneficial services provided by the environment that humans rely on such as pollination and agricultural pest control. Biodiversity generally strengthens natural pest suppression on farms (Root 1973, Snyder 2019) and increased plant diversity is well-known to support natural enemy abundance by supplementing food and habitat resources (Letourneau et al., 2011). Farmers leverage this by augmenting non-crop diversity either through managed flower patches (Morandin et al. 2014, Blaauw and Isaacs 2015, Campbell et al. 2017, Gurr et al. 2017, Alcalá Herrera et al. 2021) or by allowing weedy non-crop growth to persist (Barbercheck and Wallace 2021, Madden et al. 2021). In general, structural complexity from vegetative tissue can provide refuge for natural enemies from their own predators and alternative prey on which to feed (Landis et al. 2000, Finke and Denno 2002, Gurr et al. 2017) while nectar provisions from flowers can improve survival, longevity, and fecundity of many natural enemies (Van Rijn et al. 2006, Vattala, H.D. et al. 2006, Araj and Wratten 2015). The attractiveness of floral resources to pollen and nectar feeding insects may be determined by floral traits (Schemske and Bradshaw 1999). McGill et al. (2006) describes a trait as a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species, while a "functional trait" generally refers to a trait that specifically helps survival and reproduction, or general performance of the organism (McGill et al. 2006, Violle et al. 2007). Traits tend to be general (McGill et al. 2006) and can be similar across species, landscapes, and ecological ranges, making looking at floral traits easily moldable across research contexts (Hatt et al. 2019). Floral traits can include flower color, UV patterning, flower shape, corolla length, and presence or absence of floral spurs and/or extrafloral nectaries.

Corolla Shape

Hoverflies (Syrphidae), for example, are considered beneficial as certain species have zoophagous larvae and adults that are pollinators (Wäckers and van Rijn 2012). Hoverfly adults are nectar and pollen feeders, and females require the proteins from pollen for sexual maturation (Van Rijn et al., 2006). Floral nectar resources have also been shown to increase hoverfly longevity (Wäckers & van Rijn, 2012; H.D. Vattala et al., 2006). Hoverflies tend to be associated with "shallow" or shorter corollas, also called "open" corollas (Hogg et al. 2011, Wäckers and van Rijn 2012, Hatt et al. 2019). Campbell et al. (2012) found hoverflies using both long and short corolla flowers, but apparently the species recorded in this study all had very different feeding niches and thus different mouthparts. Flowers with short corollas, such as sweet alyssum, buckwheat, and flowers with umbelliform structure like those in Apiaceae are all highly attractive to hoverflies (Hogg et al. 2011, Wäckers and van Rijn 2012). Specifically, Wäckers & van Rijn (2012) found that florets with corolla depths of 1.6 mm or less were more suitable for hoverflies than florets deeper than 2.1mm. Other important biocontrol insects share similar preferences. For example, sweet alyssum was also found to be attractive to minute pirate bugs (Anthocoridae), tiny generalist predators that pack a biocontrol punch (Hogg et al., 2011; Fielder and Landis, 2007), as well as parasitoid wasps (Buchanan et al. 2018), which are also important natural enemies for a variety of pests. Campbell et al. (2012) also found that parasitoid wasps showed an affinity for shorter corolla flowers and were recorded 20x less often at long corolla flower plots. Flowers with long corollas tend to be coevolved with pollinators – consequently many pollinators have long proboscis mouthparts that allow them to reach nectar /pollen in flowers with long corollas (Johnson and Anderson 2010). For example, a study that compared bumblebee, parasitoid wasp, and hoverfly visitation on a short corolla, long corolla, and mixed trait flower mixes found bumblebees to prefer long corolla flowers in mixes of flowers of different corolla lengths (Campbell et al. 2012). Natural enemies might feed on nectar and pollen, but there are many who are simultaneously entomophagous. As opposed to highly coevolved nectar feeders that have specialized mouthparts shaped to access specific plants (Johnson and Anderson 2010), these more generalized feeders will have more generalized (read: less specialized) mouthparts. Size, shape, and structure of the head and mouth can either be helpful or prohibitive in accessing floral resources, depending on the morphology of the flower (Gilbert and Jervis 1998, Vattala, H.D. et al. 2006). Simply put, if the insect can't reach nectar and pollen, feeding will not be possible, precluding them from the nutritional and often necessary benefits of these resources.

Floral Color

While floral color has been shown to be attractive to insects at long range, color is not always found to be a significant factor in generating generalist predator abundance (Hatt et al. 2019). A study by Hatt et al. (2018) found hymenopteran parasitoids of certain pollen beetles were more abundant in flower patches with relatively high abundance of yellow flowers than in patches with high abundances of either white or violet flowers. Parasitoids of one kind of pollen beetle (*Melegethes* spp.) in their study system were significantly attracted to yellow flowers. Parasitoids of a different pollen beetle in their study system (*Ceutorhynchus* spp.) were specifically repelled from violet flowers (Hatt et al. 2018). Begum et al. (2004) examined survival rates of a certain parasitoid and their effectiveness of parasitizing a pest when given different colors of the same flower – white alyssum. Interestingly, they found that though both flowers were technically white sweet alyssum, survival was greater on the non-dyed, natural white alyssum than on the white alyssum that had been colored. Wackers (1994) found a certain parasitoid was attracted to yellow surfaces when starved, but preferentially landed on green surfaces if they had been sugar fed, preferences that are likely species specific. The complexity of color preference and relative attractiveness to beneficial insects suggests that more nuanced investigation might be needed to parse apart preferences of most economically and ecologically relevant beneficial insects.

UV Patterning

UV patterning, specifically a bulls-eye pattern (UV absorbing middle of flower petals with UV reflective outer area of petals) is relatively ubiquitous and is often thought to be used by insects for orienting to pollen/nectar rich areas of the inflorescence (Koski & Ashman, 2014). There is some evidence that UV patterning is associated with certain natural enemies. Lacewing abundance was correlated with UV patterning in a study by Hatt et al. (2019), but in the same study, only 2 of three species of ladybeetle this same abundance/UV pattern correlation; the other ladybeetle species' abundance was actually specifically correlated with flowers *without* UV patterning (Hatt et al. 2019). That being said, neither of these attractiveness's are considered likely in bringing insects in from far away but rather keeping them in one place (Hatt et al. 2019). Attractiveness at only short range may be useful in maintaining a population, but recruitment of natural enemies is clearly an important part of the equation. Buchanan et al. (2018) found that while sweet alyssum was attractive to parasitoids of asparagus leaf miner when it was grown in garden plots, this attractive effect was lost when the alyssum was planted as a flowering strip. In both of these planting patterns, there was no increase in biocontrol services – no significant decrease in asparagus leaf miner was detected. In a study examining potential parasitism differences on squash bugs in fields with flower borders versus control borders, egg parasitism of two squash bug species was not affected by either border treatment (Cornelius et al. 2019). Given the varied responses of different insects to floral UV patterning, investigating when and how these configurations are attractive to beneficial insects could be key in designing flower communities to bolster pest control.

Evenness

As reviewed, there are myriad correlations between natural enemies and floral traits, and natural pest suppression on farms is often bolstered through increased biodiversity (Root 1973, Snyder 2019). Even so, reliable links between biodiversity and biocontrol are still difficult to predict (Landis et al. 2000, Gurr et al. 2017). Community evenness among predators may be a metric with better predictability of biocontrol function (Crowder et al. 2010) than abundance or richness alone (Crowder et al. 2010, Snyder 2019, Blubaugh, Asplund, Smith, et al. 2021). It is not well known what exactly creates enemy evenness in an agroecosystem but knowing more about what manifests evenness in these systems may allow us to create a more tailored approach to conservation biocontrol in terms of created habitats. Managing farms to promote evenness remains a challenge (Snyder 2019), yet recent work suggests that non-crop plants could be a potential tool (Crowder and Jabbour 2014, Blubaugh et al. 2021b). One way to go about this may be a trait-based approach. Testing different combinations and iterations of floral traits and investigating if any trait or suite of traits in particularly correlated with evenness among natural enemies may provide a better baseline in creating personalized plant mixes for specific crops. By using a trait-based approach, issues with different environments may be circumvented and plant mixes could be created with trait-exhibiting plants that are able to thrive in the chosen environment without worry of introducing possibly invasive cultivars where they are not wanted. However, the feasibility and economic viability of such an approach might be prohibitive. Another option may be to refocus on plant biodiversity from a community perspective.

As mentioned in the beginning of this review, farmers often leverage the ability of plant biodiversity to recruit natural enemies by augmenting existing non-crop communities. This may either be through having managed flower patches (Morandin et al. 2014, Blaauw and Isaacs 2015, Campbell et al. 2017, Gurr et al. 2017, Alcalá Herrera et al. 2021) or by allowing weedy non-crop growth to persist (Barbercheck and Wallace 2021, Madden et al. 2021). While floral resources often work as intended to promote biological control (Letourneau et al. 2011, Gontijo et al. 2013), non-crop habitats have the potential to complicate biocontrol efforts or even backfire as well (Araj et al. 2009, Buchanan et al. 2018). For example, habitat enhancements might recruit crop pests (Tscharntke et al. 2016), bolster populations of hyperparasitoids of desired biocontrol insects (Araj et al. 2009), or attract invasive intraguild predators that inflict ecosystem disservices (Crowder and Snyder 2010). Intraguild predators, which kill and eat each other rather than herbivores (Snyder 2019), can dominate insect predator communities and undermine balancing effects of non-crop plants on natural enemies (Snyder et al. 2004, Crowder and Snyder 2010, Blubaugh et al. 2021a).

In the Southeastern United States, the red imported fire ant (*Solenopsis invicta* Buren) dominates agricultural food webs (Tschinkel and King 2013, Sáenz-Romo et al. 2019) and frequently act as an intraguild predator (Eubanks 2001). Fire ants are an exotic invasive which arrived in the United States around a century ago (Tschinkel 2006) and are a dominant species even in their natural range (Calcaterra et al. 2008). These ants are well adapted to early successional habitat (Tschinkel and King 2013) and thus often thrive under conditions of high ecological disturbance (King and Tschinkel 2008). Interestingly, red imported fire ants also do well in highly vegetated areas (Harvey and Eubanks 2004, Tschinkel and King 2013, Lewis et al. 2020). Agricultural landscapes are inherently characterized by human-mediated disturbance yet are also highly vegetated. Thus, it is important to consider how different sources of plant diversity and dominant invaders each shape the community structure of resident insect predator communities. While both weedy and intended floral resources can clearly benefit biocontrol, it is still unclear which of these two types of non-crop diversity has the strongest balancing effects on insect predator communities.

We want to examine how both intended floral diversity and weedy diversity predict the activity of a dominant invasive predator and insect predator community structure. This study aims to refine our understanding of how non-crop diversity can contribute to biocontrol efforts by determining which specific plant communities may best strengthen evenness among insect predators. Parsing apart these interactions and considering the important role evenness may play in agroecosystems will bring ecologists and growers closer to creating a more successful vision of conservation biocontrol.

CHAPTER 2

ANTS IN YOUR PLANTS: FLORAL RESOURCE DIVERSITY ON ORGANIC FARMS INCREASES INVASIVE FIRE ANTS RATHER THAN NON-INVASIVE PREDATORS[1]

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[1] Sparer, A., Madden, M., and Blubaugh, C.K. To be submitted to Food Webs.

Abstract

Increasing plant diversity in agroecosystems is well-known to strengthen pest suppression, yet reliably predicting which kinds of non-crop diversity best support biological control remains a challenge. Farmers often supplement non-crop diversity with managed flower patches or by allowing weedy non-crop growth to persist, both of which may support diverse, abundant, and balanced communities of insect predators that provide strong biocontrol services. At the same time, balance among insect predators and effectiveness of biocontrol services may be compromised by dominant predators that co-benefit from non-crop diversity. We examined whether floral resources or weedy habitat had stronger balancing effects on insect predator communities by surveying plants and insects on zucchini crops at 37 organic farms. We found that neither floral resources nor weeds affected insect predator evenness. Instead, an invasive predator, the red imported fire ant (*Solenopsis invicta* Buren), negatively predicted evenness among non-invasive insect predators. Fire ant activity increased with floral resource availability, and neither fire ants nor non-invasive predators clearly predicted removal of sentinel prey. These results suggest that floral diversity may be a less reliable predictor of biological control when invasive predators interfere with the community structure and function of non-invasive predators. Habitat management recommendations for bolstering biocontrol services should consider and potentially mitigate unintended consequences of floral resource provisions on farms where invasive predators dominate.

Keywords: evenness, plant diversity, biological control, floral resources, natural enemies, red imported fire ant

Introduction

Biodiversity generally strengthens natural pest suppression on farms (Root 1973, Snyder 2019) but precise and reliable links between biodiversity and biocontrol are still difficult to predict (Landis et al. 2000, Gurr et al. 2017). Community evenness among predators (a measure of relative abundances of species in a community) may be a metric with better predictability of biocontrol function (Crowder et al. 2010), as balanced communities are less likely to include dominant taxa that interfere with ecosystem services (Blubaugh et al. 2021a), and more likely to occupy complementary spatiotemporal niches that strengthen trophic cascades (Hillebrand et al. 2008) and stabilize them over time (Isbell et al. 2009, Wang et al. 2021). Managing farms to promote evenness remains a challenge (Snyder 2019), yet recent work suggests that non-crop plants could be a potential tool (Crowder and Jabbour 2014, Blubaugh et al. 2021b). While increased plant diversity is well-known to support natural enemy abundance by supplementing food and habitat resources (Letourneau et al., 2011), such resources may also give rise to balance among insect predators that strengthens and stabilizes patterns of pest suppression (Blubaugh et al. 2021b).

Farmers augment non-crop diversity either through managed flower patches (Morandin et al. 2014, Blaauw and Isaacs 2015, Campbell et al. 2017, Gurr et al. 2017, Alcalá Herrera et al. 2021) or by allowing weedy non-crop growth to persist (Barbercheck and Wallace 2021, Madden et al. 2021). In general, nectar provisions from flowers can improve survival, longevity, and fecundity of many natural enemy species (Van Rijn et al. 2006, Vattala, H.D. et al. 2006, Araj and Wratten 2015), while structural complexity from vegetative tissue can provide refuge for insect predators from their own predators and alternative prey on which to feed (Landis et al. 2000, Finke and Denno 2002, Gurr et al. 2017). Managed flowering plants are repeatedly found to strengthen pest control services (Albrecht et al. 2021) and can pay off economically even when they replace crops in fields (Morandin et al. 2016). However, weedy plants can also provide food and habitat resources that support crop protection without intentional or costly management (Blaix et al. 2018, Barbercheck and Wallace 2021). Only a few studies compare the relative benefits of weeds and managed flowering plants for natural enemy performance in controlled environments (Araj et al., 2009; Araj & Wratten, 2015; Jado et al., 2019 Table 1), or explicitly examine these two sources of non-crop diversity in the field (Gontijo et al. 2013, Morandin et al. 2014, Buchanan et al. 2018, Sáenz-Romo et al. 2019), Table 1).

Table 1. Experiments comparing benefits of weeds and managed floral resource plants for natural enemies.

Study	Study system	Natural enemy taxa	Non-crop plants	Results
Saenz-Romo et al. 2019	Grapes *Vitis vinifera* (Field Experiment)	Generalist predators	**Weeds:** Spontaneous weedy cover **Flowers:** Annual seed mix (*Asteraceae & Paperavaceae)*	Generalist predators at the soil surface were higher in weedy treatments than native flowering plants. No differences in natural enemies were observed in the canopy.
Araj et al. 2019	Laboratory Experiment	Parasitoid wasp *Eretmocerus mundus*	**Weeds:** White rocket (*Diplotaxis erucoides.*), and wild mustard (*Sinapis arvensis*) **Flowers:** Buckwheat, sweet alyssum	Exposure to floral resources increased *E. mundus* longevity, egg load, and fecundity significantly more than a water control, but was highest in Buckwheat (6x) and Sweet Alyssum (4x). Buckwheat increased parasitism rate of whitefly (*Bemisia tabaci*) by 72.1%.
Buchanan et al. 2018	Asparagus (*Asparagus officinalis*) (Field Experient)	Parasitoids and generalist predators	**Weeds:** Unmanaged weedy control **Flowers:** Sweet alyssum (*Lobularia maritima*), buckwheat, partridge pea *(Chamaecrista fasciculata)*	Herbivores and parasitoids were 3x higher in sweet alyssum plantings than on all other flowering plants. No differences in predators. On asparagus plants, sweet alyssum strips increased generalist predators, but not parasitoids.

Jado et al., 2019	(No-choice lab assay)	Parasitoid wasp *Aphidius colemani*	**Weeds:** White rocket (*Diplotaxis erucoides.*), and wild mustard (*Sinapis arvensis*) **Flowers:** buckwheat, alyssum, lavender (*Lavandula angustifolia*), marjoram (*Origanum vulgare*), thyme (*Origanum marjorana*), and peppermint (*Mentha piperita*)	Buckwheat increased biocontrol of GPA (green peach aphid) as well as longevity and fecundity of *A. colemani* significantly more than other plants (including the weeds).
Araj & Wratten 2015	*Brassica oleracea* (No-choice lab assay)	Aphid parasitoid (*Diaretiella rapae)*	**Weeds:** White rocket and wild mustard **Flowers:** Buckwheat, sweet alyssum	Buckwheat increased longevity, fecundity and parasitism relative to alyssum and the weedy taxa
Morandin et al. 2014	Tomato *(Lycopersicon esculentum)* (Field experiment)	Parasitoids and generalist predators	**Weeds:** Unmanaged field edges **Flowers:** Managed flowering hedgerows (native perennial shrubs & grasses)	Greater enemy richness and more parasitoids found in hedgerows than in weedy edges, though predator abundance did not differ. In crops adjacent to flowering hedgerows, more natural enemies, higher rates of parasitism, and fewer pests were observed relative to unmanaged weedy strips.
Gontijo et al. 2013	Apple (*Malus domestica*) (Field experiment)	Generalist predators: spiders, syrphids, lacewings, coccinellids, dermapterans, anthocorids, nabids	**Weeds:** Mowed spontaneous grass cover **Flowers:** Sweet alyssum	More natural enemies and fewer wooly apple aphids found in orchards with sweet alyssum strips relative to grassy controls.

While floral resources often work as intended to promote biological control (Letourneau et al. 2011, Gontijo et al. 2013), non-crop habitats have the potential to complicate biocontrol efforts or even backfire as well (Araj et al. 2009, Buchanan et al. 2018). For example, habitat enhancements might recruit crop pests (Tscharntke et al. 2016), bolster populations of hyperparasitoids of desired biocontrol insects (Araj et al. 2009), or attract invasive intraguild predators that inflict ecosystem disservices (Crowder and Snyder 2010). Intraguild predators, which kill and eat each other rather than herbivores (Snyder 2019), can dominate insect predator communities and undermine balancing effects of non-crop plants on natural enemies (Snyder et al. 2004, Crowder and Snyder 2010, Blubaugh et al. 2021a). In the Southeasten United States, the red imported fire ant (*Solenopsis invicta* Buren) dominates agricultural food webs (Tschinkel and King 2013, Sáenz-Romo et al. 2019) and frequently act as an intraguild predator (Eubanks 2001). Fire ants are an exotic invasive which arrived in the United States around a century ago (Tschinkel 2006) and are a dominant species even in their natural range (Calcaterra et al. 2008). These ants are well adapted to early successional habitat (Tschinkel and King 2013) and thus often thrive under conditions of high ecological disturbance (King and Tschinkel 2008). Interestingly, red imported fire ants also do well in highly vegetated areas (Harvey and Eubanks 2004, Tschinkel and King 2013, Lewis et al. 2020). Agricultural landscapes are inherently characterized by human-mediated disturbance yet are also highly vegetated. Thus, it is important to consider how different sources of plant diversity and dominant invaders each shape the community structure of resident insect predator communities. While both weedy and intended floral resources can clearly benefit biocontrol, it is still unclear which type of non-crop diversity (floral resources or weeds) has the strongest balancing effects on insect predator communities.

Here we examine how both intended floral diversity and weedy diversity predict the activity of a dominant invasive predator and insect predator community structure by surveying insects, flowering plants, and weeds at 37 organic farms. We predicted that both intended floral richness and weedy richness would positively predict predator community evenness (Crowder and Jabbour 2014), with weaker effects from weedy resources due to fewer available floral resources (Sutherland 2004). We predicted that evenness among non-invasive predators would decrease with the abundance of an invasive predator, the red imported fire ant, *Solenopsis invicta* Buren (Chan and Guénard 2020, Blubaugh et al. 2021a). It's currently unclear how fire ants might complicate links between non-crop plants and insect predators, due to evidence of fire ants both thriving under high disturbance (King and Tschinkel 2008) and in highly vegetated areas (Harvey and Eubanks 2004, Tschinkel and King 2013, Lewis et al. 2020). This study aims to refine our understanding of how non-crop diversity can contribute to biocontrol efforts by determining which specific plant communities may best strengthen evenness among insect predators.

Methods:

Between May and August of 2021, we sampled insects on zucchini crops (*Cucurbita pepo*) at 37 organically managed farms throughout Georgia, North Carolina and South Carolina, and recorded richness of intentionally planted flowering plants and weeds. All farms were sampled once during this season. Not all farms were USDA certified organic, but all farms used "organic" growing methods and management practices. Farms ranged from rural parcels up to 50 acres at the largest to small urban farms under one acre at the smallest.

Study system:

We chose zucchini as a focal crop due to the diverse community of herbivores that feed on this crop, as well as the challenges they pose to farmers who grow it organically. Zucchini is affected by both generalist and specialist pests that lend high pest pressure and abundant insect predator communities (Schmidt et al. 2014). Insect predators common in our system included Minute Pirate Bugs (Heteroptera: Orius), stilt-bugs (Heteroptera: Berytidae), Big Eyed Bugs (*Geocoris* sp.), damsel bugs (Heteroptera: Nabidae), ants (Hymenoptera: Formicidae), carabid beetles (Coleoptera: Carabidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), and ladybeetles

(Coleoptera: Coccinellidae*)*. In the Southeastern United States, red imported fire ants (*S. invicta)* often dominate agricultural food webs (Tschinkel and King 2013, Sáenz-Romo et al. 2019), and frequently act as intraguild predators (Eubanks 2001). Therefore, fire ants were not included in insect predator counts or diversity indices and were compared separately.

Plant sampling:

To quantify weed diversity, we identified and counted weeds within a 0.5 m^2 quadrat placed directly in front of focal plants. Five randomly selected quadrat samples were taken once per site. Plants included in "weed" sampling included both grasses and broadleaf plants. To assess non-crop intentional floral resources, we used a protocol modified from O'Connell et al. (2021). All non-weed blooming plants within a 400 m^2 area surrounding the center of the zucchini planting were recorded and identified at the family level. "Weed" is an anthropomorphic and subjective designation, and we acknowledge that many plants often defined as weeds possess important floral resources. In the context of this study, we defined "weeds" as only the plants growing in the beds of the focal plant unintentionally and these were only characterized through the quadrat survey. We defined "non-weed blooming plants" as those plants not included in weed survey by way of not growing in beds of the focal plant or other crops. Bolted or blooming crops, ornamental flowers, herbs, pollinator plantings, lawn or roadside weeds, and cover crops were all included as long as they fell within the survey area.

Insect sampling:

To measure insect predator abundance, a vacuum sample was collected at each site once during the season using a modified leaf blower with reverse air flow fitted with a mesh bag to collect insects. Surveyors sampled one row of focal crops (10 randomly selected plants) and vacuumed for 10 seconds per plant (Blubaugh et al. 2018). Mesh bags were immediately removed, shaken to move insects towards the bottom of the bag, tied closed, and placed on dry ice. Insects were then transferred to 70% EtOH until they could be identified in the lab at the family level. Pielou's evenness at the family level was calculated for all generalist predatory insects (spiders and parasitoid wasps, as well as fire ants, were excluded) using the Vegan package in R (Oksanen et al. 2009). Due to their ability to cling to plants, fire ants were quantified visually on plants, instead of in vacuum samples. Fire ants were counted by visually inspecting six leaves (two young, two middle age, and two old) and all flowers on 10 randomly selected zucchini plants in each field. Neither spiders nor parasitoid wasps were included in our analyses.

Sentinel prey assays:

To examine how floral diversity and weed diversity shape rates of biological control, we used a prey removal assay to estimate rates of removal of fruit fly pupae (*Drosophila melanogaster* Meigen). Fruit fly pupae were used as the prey item as they are a comparable size and shape as the eggs of squash bugs (*Anasa tristis* De Geer), which are the most problematic pest in our system. (Schmidt et al. 2014). We affixed twenty-five evenly dispersed frozen fruit fly pupae to cardstock measuring approximately 3 cm^2 with double-sided carpet tape on one side. Cards were then covered in sand to prevent accidental insect capture. We used paper clips to attach cards to leaves with the prey side up on five randomly selected zucchini plants per site. We removed cards after 1 day and placed them into individual plastic bags. Remaining pupae on each card were counted under a dissecting microscope and proportions of pupae removed were recorded.

Statistical analysis:

Structural Equation Model: All analyses were performed in RStudio version 2021.09.2. To evaluate links between predator community evenness, weedy non-crop richness, floral non-crop richness, and dominant invasive predator abundance, we ran a path analysis using R package piecewiseSEM (Lefcheck 2016). Path analysis allows us to evaluate and optimize multiple linear models simultaneously, and explicitly measures the relative strengths of direct and indirect effects, enabling us to clarify causal links between variables across trophic levels. Our path model evaluated the strengths and directions of links between floral resource richness, weedy non-crop richness, predator community evenness, and fire ant abundance. Component models in the path analysis included a generalized linear mixed model (GLMM) predicting non-invasive predator community evenness, which assumed a gaussian distribution, while the fire ant model assumed a negative binomial distribution (fire ant counts were over dispersed), and the predator abundance model assumed a Poisson distribution. Farm site was included in each GLMM as a random effect to account for non-independence between multiple predictor variables. Model assumptions were checked with residual plots. Path model goodness of fit was assessed with d-separation tests on Fischer's C statistic and Akaike information criterion (AIC).

Pupae Card Analysis: To investigate if predator community abundance or dominant predator (fire ant) abundance correlated with proportions of prey removed in our sentinel prey assay, we employed binomial GLMs.

Results

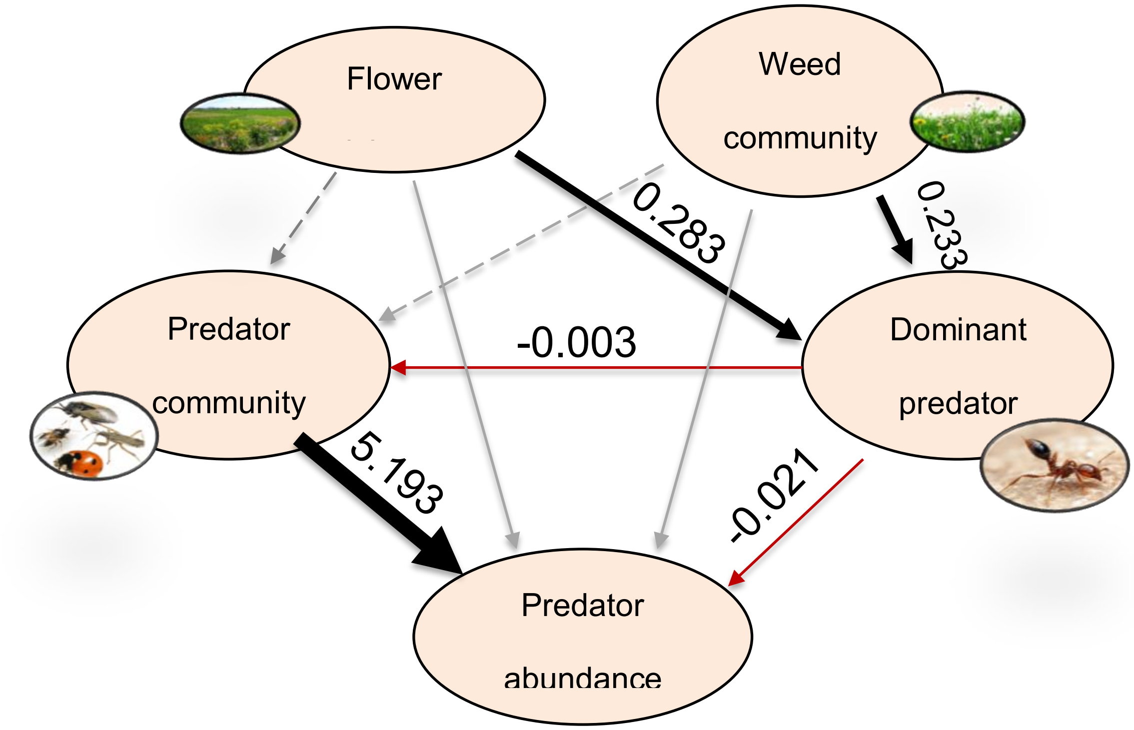

Figure 1. Structural Equation Model showing links between Weed Community Richness, Non-Crop Flower Richness, Predator Community Evenness, Predator Abundance, and Dominant Predator Abundance. Black lines indicate significant positive links, red links indicate significant negative links, dashed gray lines indicate insignificant links

Structural Equation Model: Our model provided adequate goodness of fit (Fischer's C=2.323. P-value = 0.677, 4 degrees of freedom). We found that ants benefitted from diverse blooming plants (floral richness; SE = 0.0813, p = 0.0005), but only benefitted marginally from weed richness (SE = 0.1393, P = 0.0936; Fig 1., Fig. 2,). The only significant predictor of insect predator evenness was a weak negative relationship with fire ant counts in crop foliage (Fig. 1, Fig. 3, Table 2); neither floral richness nor weed richness was a predictor of insect predator evenness (Fig. 1, Fig. 3, Table 2). Predator community evenness was a strong and significant predictor of predator abundance while fire ants had a negative direct effect on predator abundance. Path coefficients and pseudo-R^2s can be found in Tables 2 and 3.

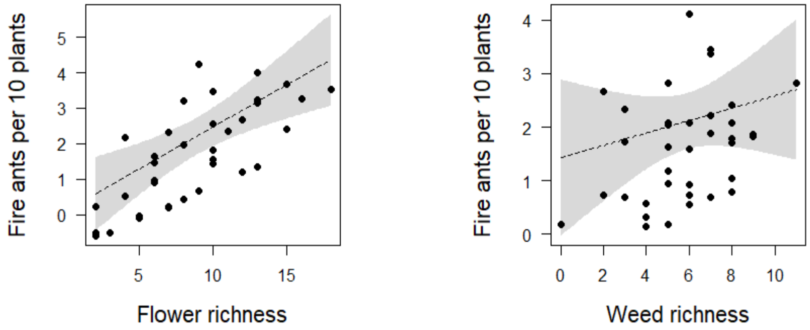

Figure 2. Relationships Between Fire Ant Abundance and Either Floral Richness (A) or Weed Richness (B). Grey shading represents a 95% confidence interval around the regression line.

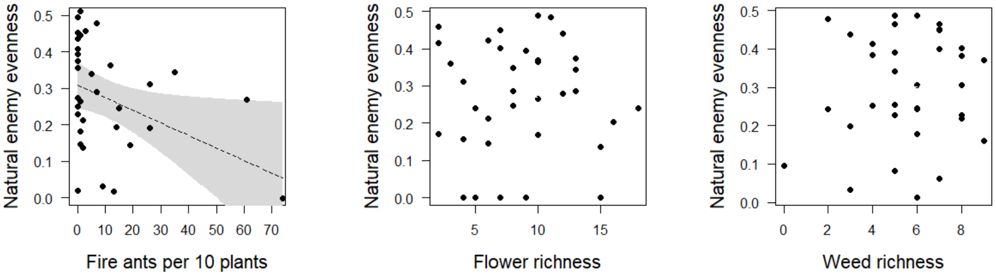

Figure 3. Relationships between Insect Predator Evenness and Fire Ant Abundance (A), Floral Richness (B), and Weed Richness (C). Grey shading represents a 95% confidence interval around the regression line.

Table 2: Path analysis output examining direct and indirect links between Predator Abundance, Predator Evenness, Foliar Ants, Weed Richness, and Floral Richness, including path coefficients, standard errors, and p values. Significant P values ($P < 0.05$) are in bold.

Response	**Predictor**	**Coefficient**	**Standard Error**	**P value**
Predator Abundance	Predator evenness	5.1928	0.9173	**<0.001**
	Foliar Ants	-0.0177	0.0092	**0.0541**
	Floral Richness	-0.0249	0.031	0.4226
Predator Evenness	Foliar Ants	-0.0028	0.0015	0.072
Foliar Ants	Floral Richness	0.2835	0.0813	**0.0005**
	Weed Richness	0.2336	0.1393	0.0936

Table 3: Marginal R^2 (total variation explained by fixed effects) and Conditional R^2 (total variation explained by the entire model, including random effects) for each of the response variables in our path analysis.

Model	**n**	**Marginal R^2**	**Conditional R^2**
Predator Count	37	0.69	0.69
Predator Evenness	37	0.09	0.89
Foliar Ants	37	0.34	0.99

Sentinel prey removal: There was no significant relationship between proportion of pupae removed (prey removal) and non-invasive predator abundance (Estimate = 0.007, SE = 0.021, Z = -0.331, P = 0.741, pseudo-R^2=-0.007; Figure 4A). There was also no significant relationship between prey removal and dominant predator (fire ant) abundance (Estimate = 0.013, SE = 0.021, Z = 0.634, P = 0.526, pseudo-R^2=-0.035; Figure 4B).

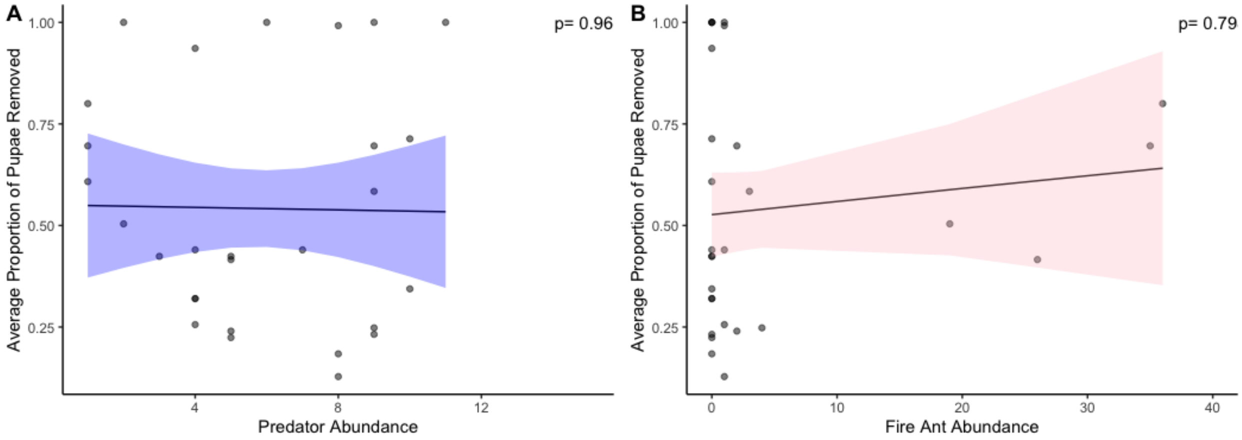

Figure 4: Relationships of Predator abundance and fire ant abundance to prey Removal. Neither predator abundance (A) nor fire ant abundance (B) significantly affects prey removal, with p=0.96 and p=0.79 respectively. Points show raw data, and line and ribbons show fitted model with standard error.

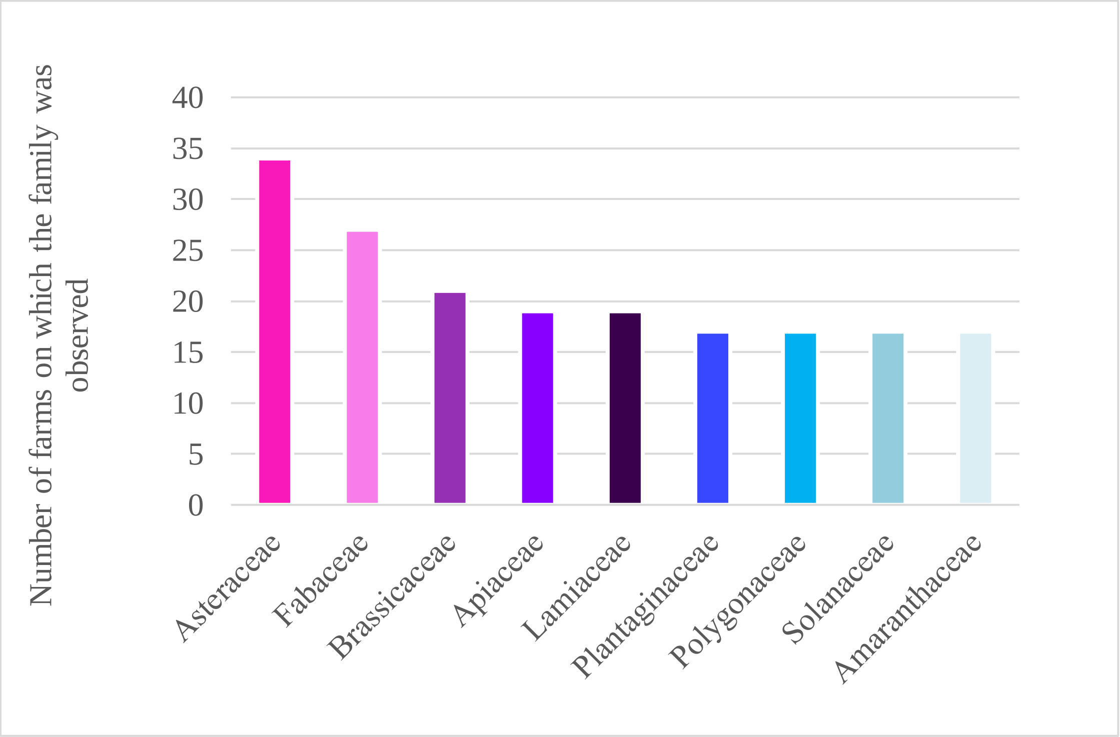

Figure 5: Most Commonly Encountered Plant Families in Intentionally Managed Plant Survey

Figure 5. Personal in-field observation of predation of sentinel pupae by imported fire ants *(Solenopsis invicta).*

Discussion:

Plant diversity often strengthens predator diversity and biological control, yet varying outcomes across studies still preclude highly specific and accurate planting recommendations for farmers (Holmes and Blubaugh, in review). Insect predator evenness might be a more reliable metric linking insect diversity (Crowder et al. 2010), plant diversity, and pest suppression (Blubaugh et al. 2021a,b), but it is not yet clear what plant communities are best at promoting evenness (Snyder 2019). We evaluated weedy plants and intentional/managed floral resources on 37 organic farms across Georgia, North Carolina, and South Carolina to determine which sources of non-crop plant diversity most strongly predicted insect predator community structure. Rather than supporting insect predator evenness, we found that flowering non-crop plants directly benefitted a dominant invasive predator, the red imported fire ant.

Evidence is mounting that dominant invasive predators might interfere in relationships between biodiversity and biocontrol (Snyder et al. 2004, Blubaugh et al. 2021a, Li et al. 2021, Blubaugh et al. 2022). Invasive insect predators tend to share characteristics that enable their domination of insect predator communities, such as disturbance tolerance, competitiveness, and frequent intraguild predation (Snyder and Evans 2006, Crowder and Snyder 2010). For example, the introduction of exotic lady beetles for biocontrol has unintentionally displaced populations of native lady beetles (Snyder et al. 2004, Rondoni et al. 2021). This is thought to be a result of some combination of the exotic predators outcompeting natives for aphid prey and higher frequencies of intraguild predation on native coccinellids (Rondoni et al. 2021). It should be noted that while lady beetles were collected in our insect samples, no adult *Harmonia axyridis* (a common, dominant exotic lady beetle), were found (See Appendix). In agroecosystems in the Pacific Northwestern United States, another dominant invasive predator, the ground beetle *Pterostichus melanarius* Illiger, benefitted from non-crop diversity, disrupting links between non-crop plants and evenness among native natural enemies (Blubaugh et al. 2021a). In the Southeastern USA, vegetative cover attracts red imported fire ants during the heat of the summer and displaces native weed seed predators to sub-optimal microclimates (Blubaugh et al. 2022). Clearly, non-crop plantings intended to strengthen insect predator diversity can backfire when dominant and invasive predators are added to the mix. Weedy plants and intentionally managed floral resource patches each contain food and habitat resources that could be exploited by a diversity of native natural enemies; but in our study, fire ants had stronger links with floral resources. While flowering non-crop plants are expected to benefit natural enemies generally, invasive fire ants may dominate these resources and exclude native insect predators from the food and habitat resources they provide (Eubanks et al. 2002). We observed asters most commonly in our intentional floral surveys

(Figure 5), some of which have nectar and pollen resources that are readily accessible to ants (van Rijn and Wäckers 2016). Interestingly, Fabaceae (Figure 5), which commonly have Extra-Floral Nectaries (EFNs) (Marazzi et al. 2012, Gonzalez and Marazzi 2018) that many ants feed on (Bentley 1977, Lanza et al. 1993) was the second most commonly encountered family. The shallow corolla structure of flowers in the family Apiaceae are well accessed by insects with unspecialized mouthparts such as hoverflies (Hogg et al. 2011, Wäckers and van Rijn 2012) and anthocorids (Fiedler and Landis 2007, Hogg et al. 2011). Hymenopteran parasitoids (Buchanan et al. 2018), also possessing generalist mouthparts, easily access and feed from the shallow flowers of plants in Brassicaceae. It would follow they would also be accessible to the generalized mandibulate mouthparts of ants. This wealth of accessible resources could be driving ants towards managed floral patches. Alternatively, asters and other flowering plants may host non-pest herbivorous arthropods on which *S. invicta* can opportunistically feed (Gurr et al. 2017). Managed floral resources may also be important for *S. invicta* in that they provide untilled habitat (Morandin and Kremen 2013, King and Tschinkel 2016). Weedy communities are more aggressively managed and so less likely to be allowed to grow to a mature flowering stage (McErlich and Boydston 2014). While fire ants are disturbance-associated in natural areas (King and Tschinkel 2016), they are more abundant in agricultural systems at sites with lots of perennial untilled habitat, as frequent tillage destroys their colonies (Tillman et al. 2004).

Ants dismantled predicted relationships between plant diversity and insect predator evenness, yet it is not clear from our study that this comes at a cost to biological control services. In fact, ants have been used to control crop pests across the globe for hundreds of years (Wielgoss et al. 2014, Frizzo et al. 2020, Anjos et al. 2022). Fire ants engage in ant-hemipteran mutualism, tending honeydew-producing hemipterans like aphids, and patrolling plants to remove other herbivores and predators (Styrsky and Eubanks 2010). While aphids sometimes cause crop damage and vector disease (Westwood and Stevens 2010), ant-aphid mutualisms often lead to an overall benefit to the colonized plant (Styrsky and Eubanks 2007). We did not find significant links between prey removal and either fire ant abundance or non-invasive predators, but we frequently observed ants eating the sentinel prey in the field (Sparer, personal observation, Fig. 6). Indeed, fire ants have been recorded having beneficial effects on collards (Harvey and Eubanks 2004), soy (Eubanks 2001, Styrsky et al. 2006), and cotton (Eubanks 2001, Harvey and Eubanks 2004, Styrsky et al. 2006). In systems where invasive predators dominate and disrupt biodiversity/biocontrol relationships, it will be important to weigh both the potential benefits they have for biocontrol alongside the costs of interfering with ecosystem services by native insect predators.

The enigmatic effects of invasive predators in agroecosystems complicate efforts to deliver clear recommendations for growers to realize benefits from cultivating biodiversity. Farmers are often reluctant to invest in non-crop habitat that is costly to establish and maintain (Morandin et al. 2016), but tolerating spontaneous diversity from non-threatening weeds may be a low-cost way to increase biodiversity benefits (Madden et al. 2021, Balfour and Ratnieks 2022). Indeed, weeds take time and labor to remove (McErlich and Boydston 2014) and leaving them could be an economic boon if they can successfully act as predator refugia without compromising yields (Blaix et al. 2018). For example, in eggplant, moderate levels of weed growth reduced pests with negligible costs to productivity (Madden et al., 2021). Reducing tillage, a common method of weed control, can lead to more abundant and evenly distributed natural enemy communities (Jabbour et al., 2016; but see Rowen et al., 2020).

Given our results and the ubiquity of invasive predators in agroecosystems (Snyder and Evans 2006, Crowder and Snyder 2010, Blubaugh et al. 2021a) cultivating diversity among predators with flowering plants may be a challenge (Blubaugh et al. 2021a) and pivoting focus to spontaneous diversity for natural enemy recruitment could be a tenable, lower-risk option (Araj and Wratten 2015). Of course, flower patches are desirable for a multitude of reasons beyond creating harmony among insect predators. For example, natural enemies that use floral resources often have similar preferences to bees (Rowe et al. 2021) and intentional planting of flowers is well-known to improve pollination services (Nicholls and Altieri 2013, Feltham et al. 2015, Jönsson et al. 2015, Campbell et al. 2017). Farmers may also sell flowers and herbs in value-added products such as bouquets, arrangements, and teas (Ernst and Durbin 2022) to improve the income-generating potential of floral diversity (Jones and Sieving 2006, Altieri et al. 2014). Recommendations for managing agricultural biodiversity must be delivered with forthright illustration of complex of ecosystem services and disservices, with a keen consideration for the economic outcomes of such investments (Huss et al. 2022).

Our study sought to identify the birthplace of insect predator evenness on organic farms, but we instead discovered that relationships between plant diversity and insect predator diversity may be obfuscated in the presence of dominant invasive predators. Future studies could employ fire ant exclusion treatments to remove interference by dominant predators and evaluate whether plant diversity might indeed cultivate balance among native insect predators in their absence. Ant exclusion will also help to clarify the relative costs and benefits of dominant predators for biocontrol. In areas dominant predators reign, it will be necessary to choose whether to permit domination in biological control services, or to manage and eliminate invaders, prioritizing biocontrol services by diverse native insect predators.

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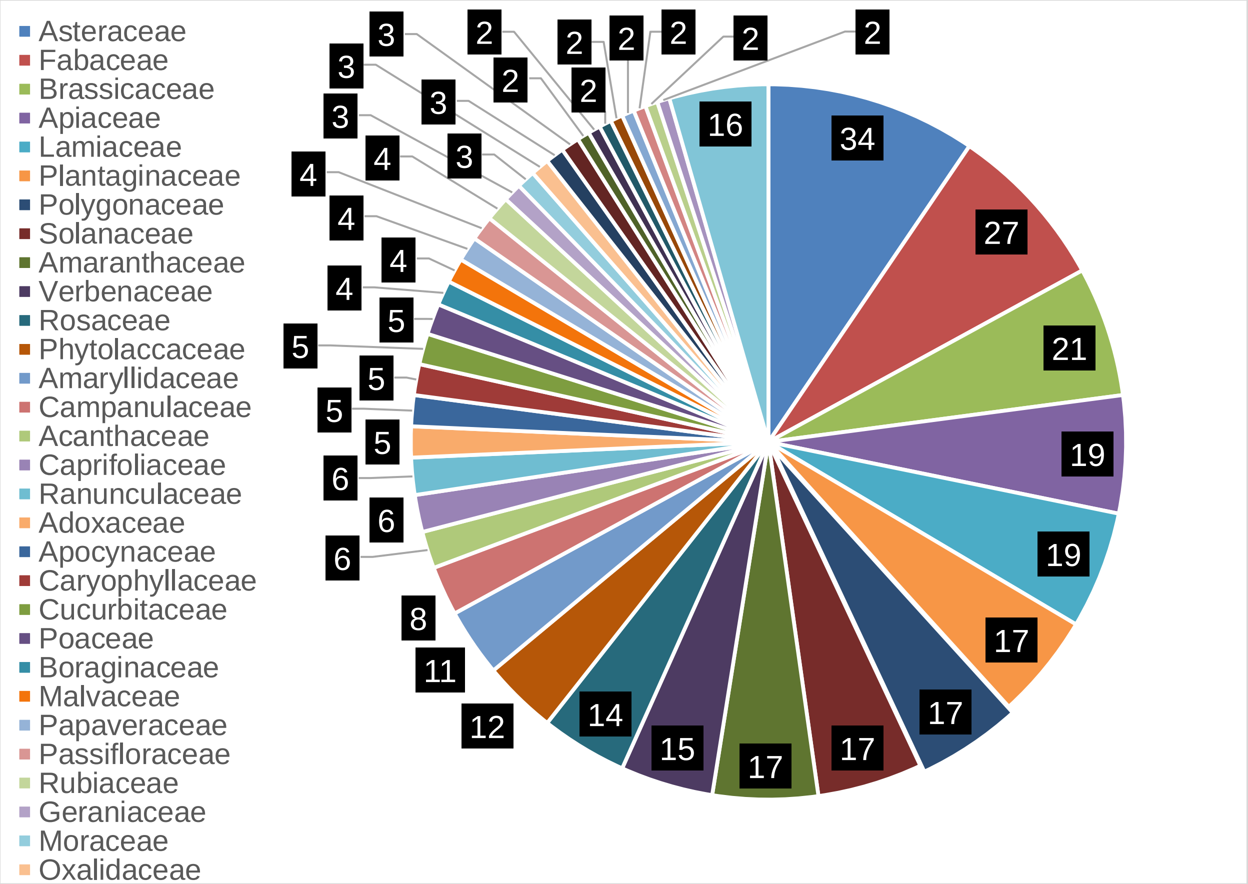
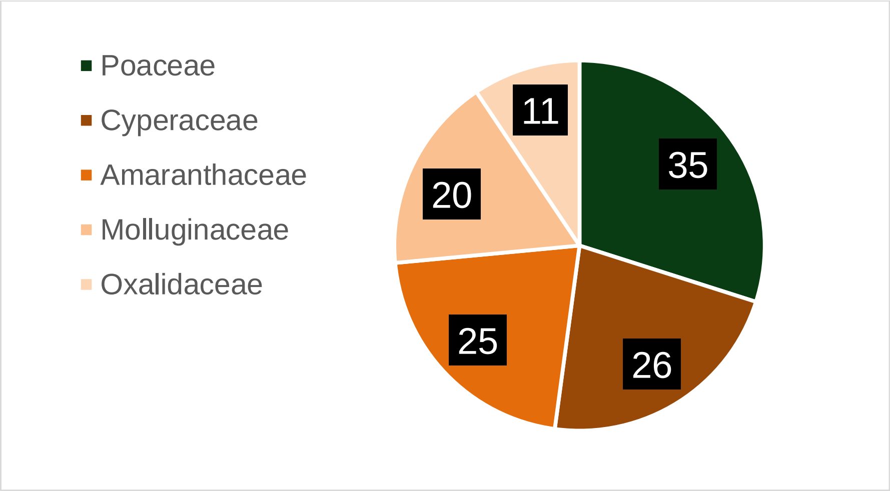
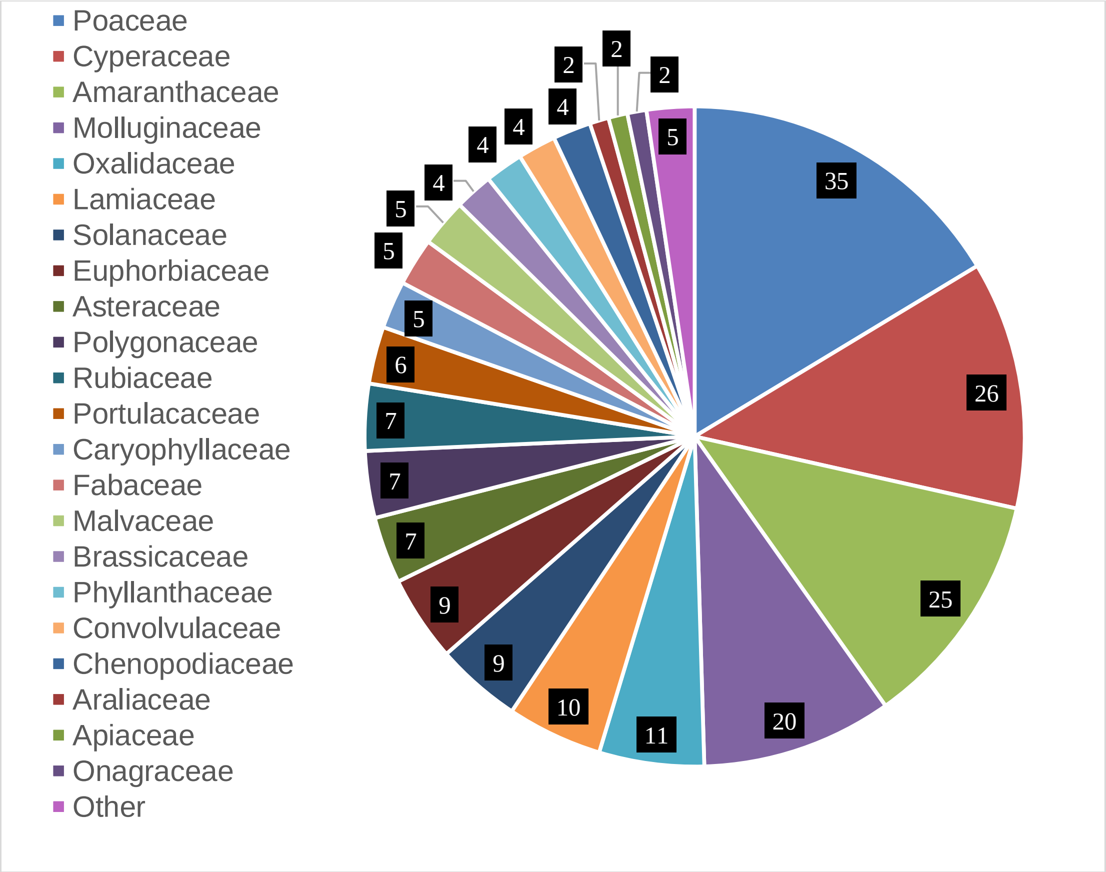
APPENDIX



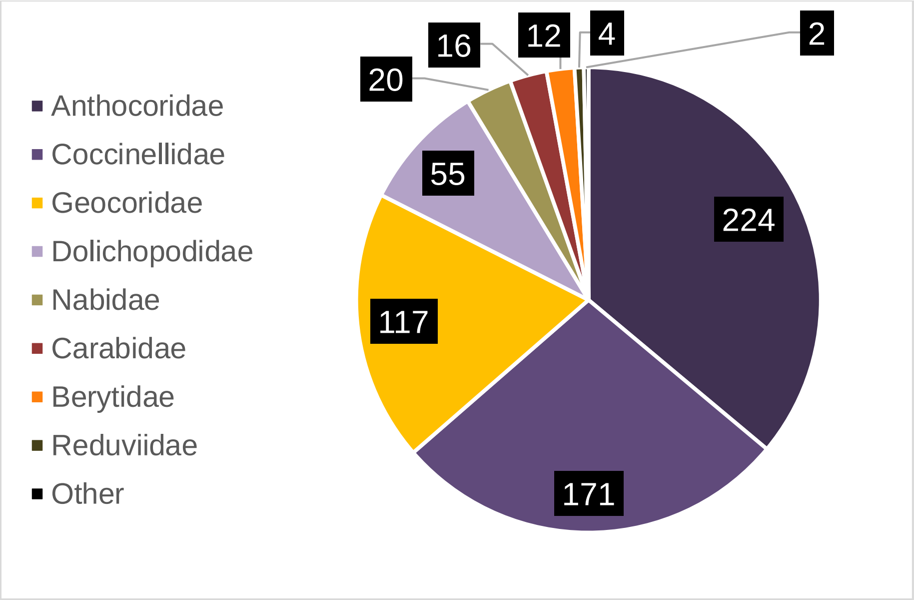
Supplemental Figure 1: Most Commonly Encountered Non-Crop Plant Families-Expanded. Data labels represent number of farms on which each family was observed.



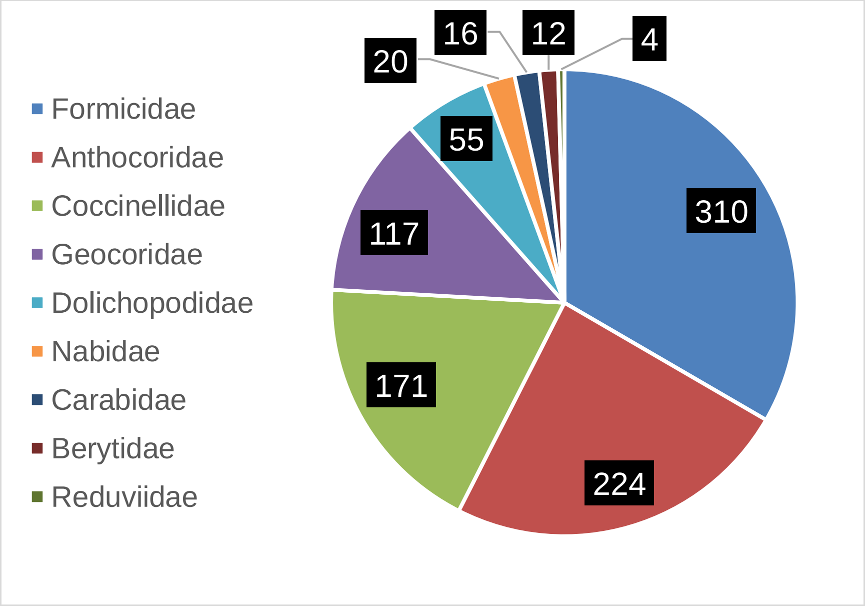
Supplemental Figure 2: Most Commonly Encountered Weed Families. Data labels represent number of farms on which each family was observed.



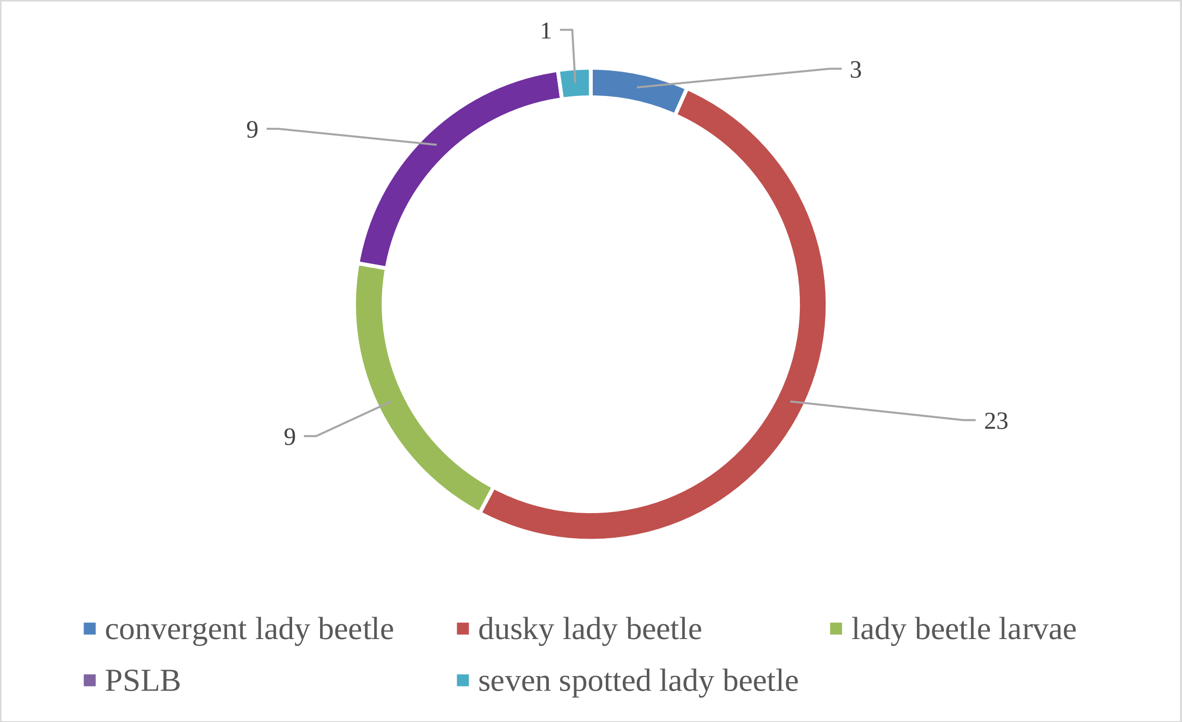
Supplemental Figure 3: Most Commonly Encountered Weed Families-Expanded. Data labels represent number of farms on which each family was observed.



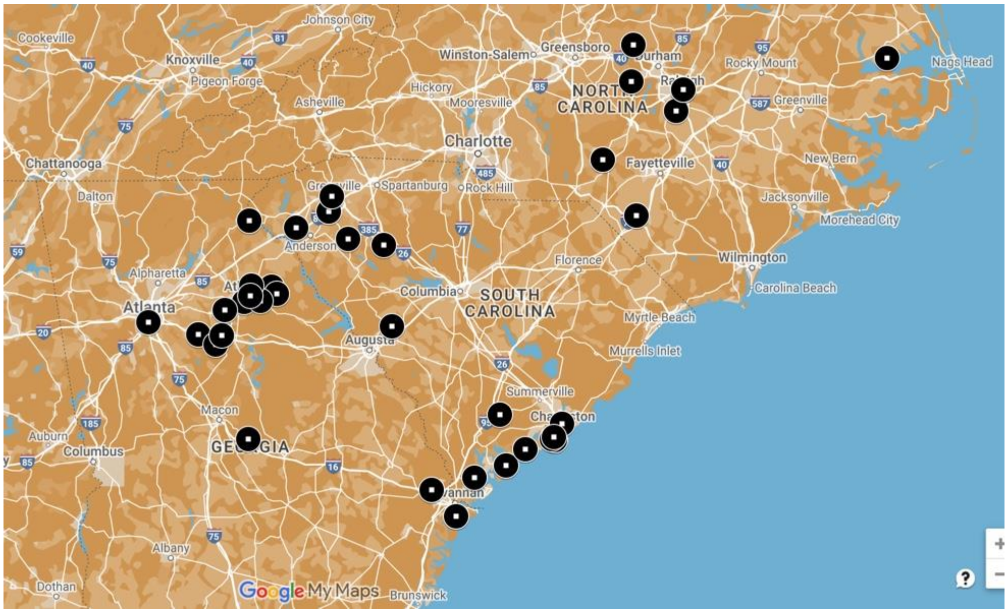
Supplemental Figure 4: Most Commonly Encountered Natural Enemy Taxa – Ants Removed. Data from DVAC Sampling. Data labels represent number of farms on which each family was observed.



Supplemental Figure 5: Most Commonly Encountered Natural Enemy Taxa – Ants Included. Data from DVAC Sampling. Data labels represent number of farms on which each family was observed.



Supplemental Figure 6: Predatory Coccinellids found in DVAC Samples. Number labels refer to amount of individuals in the sample.



Supplemental Figure 7: Map of farms surveyed in Georgia, South Carolina and North Carolina.