COVER CROPS FOR CONSERVATION BIOLOGICAL CONTROL IN COTTON AGROECOSYSTEMS

by

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(Under the Direction of Jason M. Schmidt)

ABSTRACT

Current intensive agricultural management threatens sustainability by increased land use and practices that restrict local biodiversity. Habitat management is advocated to restore biodiversity to agricultural systems and improve ecosystem functions such as biological control. We assessed the effects of cover crops on arthropods (predators and pests), their function, and cotton production during the 2017 and 2018 growing seasons. Growing cotton into cover crop residue significantly augmented predator abundance and diversity, as well as altered both community composition and prey consumption in the early growing season. Cotton grown into a rye cover crops reduced early thrips pressure and lowered boll damage when stink bug pressure was high, as well as maintained competitive levels of cotton production. Our results suggest cover crops build stable early season natural enemy communities contributing to natural pest management and crop protection.

INDEX WORDS: Cover crops, Conservation biological control, Natural enemies, Cotton, Biodiversity, Community function

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DEDICATION

I would like to dedicate this work to my family and friends. Their constant support has allowed me to take on new challenges and encouraged me to do what I love.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Current agricultural practices can have negative effects on the sustainability of agricultural ecosystems due to high synthetic inputs and continued degradation of soil health. There is a need for strategies that can improve the sustainability of these systems and increase reliance on more ecologically friendly management practices, such as those provided by biological processes. Managing habitat in and around agricultural fields can help restore biodiversity and improve the functioning of services such as natural pest control. This research focuses on the use of cover crops to promote biological control within cotton agroecosystems, as well as their influence on cotton production. It is one of the first to investigate links between habitat complexity (cover crops), predator communities, pests, and production, focusing on how biodiversity and subsequent function of natural enemy communities is influenced by cover crop use. We use molecular tools to quantify interactions between diverse predator communities and both pest and non-pest prey items throughout cotton development. This work will improve our understanding of cover crops used for conservation biological control, as well as predator function in agroecosystems.

Current issues in agriculture

Large scale intensive agriculture is common practice for meeting food and fiber demands of our growing human populations (Fedoroff et al., 2010; Matson et al., 1997; Tilman et al., 2011). Increases in land use area (Foley et al., 2005), chemical pesticides, and fertilizer inputs (Matson et al., 1997) threaten the sustainability of these systems for long term production through biodiversity loss (Tscharntke et al., 2005), nutrient pollution (Dupas et al., 2015), and reduction of soil quality (Stavi & Lal, 2015). It has also been shown that effects of landscape simplification are seen most drastically in the higher trophic levels (Purtauf et al., 2005), further exacerbating pest problems. A current challenge is the need for reducing dependence on synthetic chemical and mineral inputs, while maintaining high production levels (Tilman et al. 2011; Strassburg et al., 2014; Gurr et al., 2017). To do this, a shift has been proposed toward agricultural practices that promote ecological functions (i.e. soil fertility, pest control, pollination), where anthropogenic inputs are balanced with ecological restoration that rebuilds natural regulatory processes and services (Wittwer et al., 2017).

Biodiversity-ecosystem function

Biodiversity is considered a primary factor influencing the functioning of ecological communities (Tilman et al., 2014). Since Elton (1958) proposed that improved diversity of habitat results in increased ecosystem stability and health, an entire area of research has evolved to examine the relationships between biodiversity and the functioning and stability of ecosystems (Altieri, 1991, 1999; McLaughlin and Mineau, 1995; Duffy, 2002; Cardinale et al., 2003, 2012; Tscharntke et al., 2005; Snyder and Tylianakis, 2012; Tilman et al., 2014; Wood et al., 2015; Pillai et al., 2019; Synder, 2019). Foundational work in this area focused on plant community diversity and function (Tilman et al., 1996, 1997; Hooper &Vitousek 1997). Authors of these initial works postulated that increased diversity of species correlates with plant trait diversity, therefore improving the number and magnitude of ecosystem functions. At the level of primary producers, current research shows mostly support for diversity enhanced productivity, stability, and resistance to disturbance and invasion (Tilman et al., 2014). Continued work has revealed several potential mechanisms for a biodiversity ecosystem function and stability relationship, including: sampling effect (Huston, 1997), niche complementarity (Cardinale et al., 2007), functional overlap or redundancy (Rosenfeld, 2002), and competitive inhibition of invaders (Fargione et al., 2003). In terms of the sampling effect, the direction in which function is altered is dependent on chance, where a particularly productive species may be found in ecosystem with increased diversity, but a non-productive species which competes with existing taxa may be present, resulting in a negative effect on overall productivity and function. Increased biodiversity generally improves productivity, particularly in long term experiments (Cardinale et al., 2006, 2007). The stability of ecosystems is also influenced by diversity, where high diversity may provide "insurance" against disturbance or temporal fluctuations (Loreau et al., 2003). Increasing the number of species in an area often results in niche overlap or redundancy in particular functions (Blüthgen and Klein, 2011). With this redundancy, loss of a single species does not necessarily result in loss of function. Increasing biodiversity increases the number of different species in an area, forcing the available niche space in any given ecosystem to be exploited as compared to lower diversity systems (Lehman and Tilman, 2000; Th´ebault & Loreau 2003). A positive side-effect of diversity filling up niche space is more resilience to invasion by non-native or non-established species (Elton 1958). Building on the established biodiversity-ecosystem function literature in plant communities, current research investigates the impacts of biodiversity on higher trophic levels, especially in economically important agricultural ecosystems (Landis et al., 2000, 2017; Crowder and Jabbour, 2014; Tscharntke et al., 2005, 2012).

Aside from the production of food and fiber, agricultural systems can provide a number of ecosystem services, or services valuable to human well-being and underpinned by biological processes (Daryanto et al., 2018; Zhang et al., 2007). Some examples include groundwater recharge (Wada et al., 2010), carbon fixation for the improvement of soil health (Poeplau and Don, 2015) and mitigation of climate change (Kaye and Quemada, 2017). Some of the most well studied and economically significant include those mediated by arthropods: biological control of insect pests, and pollination (Perovic et al., 2017; Isaacs et al., 2009). Focusing on promoting and preserving arthropod mediated services is especially important since there is strong evidence that diversity at every trophic level is declining in agricultural systems due to loss of habitat, pollution, and climate change (Geiger et al., 2010; Sanchez-Bayo and Wyckhuys, 2019). Declines in biodiversity are repeatedly linked to subsequent loss of function such as biological control (Bianchi et al., 2006; Gardiner et al., 2009). Researchers agree that increasing plant diversity in agricultural landscapes generally leads to increased populations of natural enemies and reductions in pest pressure (Letourneau et al., 2011). But, several studies have found that reduced biodiversity can disrupt food webs with negative implications for pest suppression (Tylianakis et al., 2007; Schmitz and Barton, 2014), though increases in biodiversity can also hinder the effects of trophic cascades which serve as the foundation for biological control (Finke and Denno, 2004).

The ecological “niche” and how different species occupy or share niche space is central to understanding the magnitude and direction of change in predator function in response to increased biodiversity (Whittaker et al., 1973; Snyder et al., 2006; Schmitz, 2007). Predators which fill complementary niche space may improve the overall consumption and suppression of pests compared to a single species alone (Straub et al., 2008), due to additional predators feeding on different pest species. Therefore, by increasing the variety of natural enemies, a greater range of pests may be suppressed as opposed to increased suppression of a single pest (Denoth et al., 2002). Predators may also vary in their seasonal or temporal niche space, such as when complimentary predators are active at night and another during the day, or in the early season and the late season. This may result in more comprehensive pest suppression without a substantial increase in interactions between predators (Pfannenstiel and Yeargan, 2002). Even when predators share a similar temporal niche space, they may still vary in their hunting mode or habitat preferences resulting in increased capture rate of pests compared to either predator individually (Schmitz, 2009; Northfield et al., 2017). An example would be an aphid dropping from the plant to avoid a lady beetle predator and being consumed by a ground beetle in a form of predator-predator facilitation (Losey and Denno, 1998). Conversely, increases in diversity can increase the rate at which natural enemies feed or parasitize one another (Symondson et al., 2002). These effects may be reduced by an abundance of extra-guild prey, since predators often feed on other predators when other prey items are scarce (Polis et al., 1989). Therefore, it is important to understand how larger groups of species interact with one another and how these interactions determine community and ecosystem functioning.

Habitat Management

The concept of habitat management is grounded in the biodiversity ecosystem function theory (Gurr et al., 2017; Alteri, 2000). The goal is to reduce pest densities in agricultural fields through provisioning of natural or semi-natural habitat, providing benefits to natural enemies or hindering pests (Gurr et al., 2017; Hassan et al., 2016). Implementing habitat management in agriculture dates back thousands of years. There is evidence of manipulating habitat for biological control as far back as 300 A.D, where weaver ants (Genus: *Oecophylla*) nests were manipulated in Asian fruit orchards to the benefit of farmers (Barzman et al., 1999). Chinese farmers have used straw shelters for 2000 years to mitigate the effects of annual disturbance and provide overwintering sites for spider communities (Dong and Xu 1984). Burmese farmers would often use bamboo rods placed between trees in an orchard to facilitate movement of Oecophylla ants between trees to control citrus caterpillars (Emden 1989). More recently, Gurr et al. (2000) proposed the concept of manipulating habitat as a form of "integrative biocontrol" to support sustainability and natural service provisioning in more modern farming systems. Much work has been done since to identify key resources required by natural enemies which may improve their effectiveness as biocontrol agents (Letourneau et al., 2011).

Resources provided to natural enemies by the addition or management of habitat include shelter, nectar, alternative prey/host, and pollen (referred to as SNAP) (Gurr et al., 2017; Gonzalez-Chang et al., 2019; Landis, 2000). Several habitat management strategies have been assessed for their ability to provide these resources to natural enemy communities in hopes of improving biological control function. Beetle banks and hedgerows are common habitat management tactics that provide shelter resources to natural enemies (Collins et al., 2003; Maudsley, 2000). The addition of these types of habitats can improve the overwintering survival of many ground dwelling arthropods such as spiders and beetles (Collins et al., 2003), whose populations would otherwise be negatively affected by the end of season disturbance associated with annual cropping systems. Adding habitat in this way provides areas where natural enemies can continue to build or sustain their populations when cropping areas are fallow (Geiger et al., 2009). In addition to overwintering sites, provisioned habitat resources can act as wind breaks (Ricci et al., 2009), as well as mitigate against extreme temperatures in the summer and winter months (Pywell et al., 2005; Sanchez et al., 2010). Field margins, including hedgerows and banker plants (beetle banks), can provide habitat resources, but can also be used to supply additional resources to natural enemies in the form of nectar when flowering plants are used as a margin (Gurr 2017, Begg et al., 2017, Shields et al., 2019). Nectar resources of plants (floral and extrafloral) can be an important source of carbohydrates, which may benefit predators and parasitoids by increasing lifespan (Nafziger and Fadamiro, 2011), fecundity (Pumarino et al., 2012), female ratio of the natural enemy population (Berndt and Wratten, 2005) and improving fitness of enemies for effective parasitism and predation (Mathews et al., 2007; Zehnder et al., 2007). Additionally, having flowering plants nearby can provide pollen as a source of proteins and amino acids which can have similarly beneficial effects on longevity, reproduction, and fitness (Pfannenstiel, 2012; Vandekerkhove and De Clercq, 2010). Additionally, habitat management strategies can improve the provisioning of alternative prey. Due to the nature of monoculture annual production and the end of season removal of habitat, pest species can recruit more quickly and effectively to crop hosts than natural enemies. Often, predators and parasitoids will respond to increasing herbivore densities in crop habitat but are unable to effectively control pest populations after they have peaked. By using habitat management in and around agricultural fields, natural enemies can have a source of available prey items when there is little or no cropping habitat to support additional prey items in field. These strategies can bolster natural enemy communities before the arrival of economic pests (Gomez-Marco et al., 2016, Manandhar et al., 2017), allowing for responsive feeding on target pests at colonization (Athey et al., 2016; Harwood et al., 2007, 2009), and a delay of herbivore establishment (Gomez-Marco et al., 2016). Although different taxa can respond differently to provisioning of different resources, many predators will respond positively to a combination of additional resources and it is important to select strategies that provide multiple resources, encouraging the greatest positive effect on natural enemy communities and pest control function, in addition to other ecosystem services such as pollination and soil health.

Studies repeatedly show improving diversity of vegetation at the local scale has positive impacts on natural enemy communities (Letourneau et al., 2011). For example, Schmidt et al. (2004) found that adding straw mulch to wheat fields can improve spider density while reducing populations of aphids by as much as 25 percent. In a similar study, straw mulch in field was able to reduce the abundance of all life stages of Colorado potato beetle compared to a non-mulched control (Zehnder and Hough-Goldstein, 1990). The use of native plants on field margins was shown to improve the abundance and fecundity of *Coleomegilla maculata* in sweet corn fields (Cottrell and Yeargan, 1999). Yet, reviews of the responses of natural enemies or biological control of pests have found that increasing the diversity of vegetation in agricultural areas can have positive, negative, or neutral effects on pest control, even when natural enemy communities are improved (Snyder and Tyliankis, 2012). This is likely a result of the complexity of interactions between existing species that occur when biodiversity is altered, as discussed above. Therefore, there is a need for understanding the mechanisms by which habitat management practices can provide natural pest suppression through natural enemy function (top-down), or changes in pest feeding or recruitment behavior (bottom-up).

The reduction of pest pressure associated with managing habitat in and around agricultural fields can be direct or indirect, and is often thought of in terms of top-down and bottom-up trophic effects (Gonzalez-Chang et al., 2019). Indeed, Root 1973 proposed two primary mechanisms for an observed reduction of pest pressure in response to increasing habitat complexity in a collard system. The first known as the “resource concentration hypothesis” postulates that increasing habitat complexity and reduction in the density and simplicity of resources can inhibit pests’ ability to effectively locate and actively feed on crop host plants. Bottom-up effects can work through the disruption of host searching capacity of pests by masking chemical or visual cues, trapping or enticing pests to non-crop plant species, restricting movement of pests with vegetation “walls”, or changing volatile cues of the host plant (Gardarin et al., 2018). A second mechanism, described as the “enemies’ hypothesis”, serves as the foundation for much of the habitat management literature, and suggests that more complex systems provide resources to natural enemies to a greater degree than agricultural pest species, thereby increasing the effectiveness of natural enemies in providing natural pest control (Root 1973; Russell, 1989). There has been extensive work in identifying the effect of habitat management on natural enemy communities and associated pests, with recurring attempts to link increases in abundances or diversity of natural enemies to subsequently reduced pest pressure (Haseeb et al., 2018; Harrison et al., 2018; Whitehouse et al., 2017; Moriera et al., 2016). Yet, it is still often unclear which of these mechanisms are responsible for reductions in pest pressure observed in the field, or how the combined effect of top-down and bottom-up mechanisms influence the suppression of pests. There is a need for studies that can quantify contributions of natural enemy functioning or habitat changes to reductions in pest pressure in applied settings.

Cover crops

Cover crops were initially defined as a crop grown with the specific purpose of covering the ground to reduce the risk and impact of soil erosion and loss of nutrients through leaching and runoff (Parker, 1915; Pieters and McKee, 1938). The purpose of cover crops has since been expanded to include a number of beneficial ecosystem services in agricultural systems (Daryanto et al., 2018; Duzy & Kornecki, 2017; Adhikari et al., 2017, Hartwig and Ammon, 2002). Some of the most common uses now include nitrogen supplementation by legume cover crops (Wilson et al., 2019), nutrient sequestration (Daryanto et al., 2018), improving soil organic carbon

(Poeplau and Don, 2015), weed control and yield improvement (Toler et al., 2019), and recently for mitigation of climate change effects (Kaye and Quemada, 2017).

The use of cover crops is gaining traction as a habitat management strategy to ecosystem services in both annual and perennial agricultural systems. In 2012, the National Wildlife Federation called for increasing the amount of cover cropped land in the US from 4 million ha to 40 million ha nationwide (Bryant et al., 2013; Hamilton et al., 2017). In 2014, the USDA Natural Resource Conservation Service called for a doubling of cover cropped land from 4 million ha to 8 million ha by 2020 (SARE 2014). Although progress has been made, current cover crop use accounts for about 2% of land used for row crops (USDA NASS 2014). Grower reluctance to adopt cover cropping practices stems from the perceived risk associated with cover crop use (Dunn et al., 2016), both economic risk and the risk of providing resources to pest populations. Recent studies have shown the benefit of cover crops can potentially outweigh the economic risk through proper planting and management practices (Adhikari et al., 2017; Duzy & Kornecki 2017). Further research is needed to understand the mechanisms by which cover cropping affects key pests and natural enemies in cotton cropping systems in the southeast US, and if these changes impact natural enemy function and crop production. A recent review of the methodology of many of these studies showed that researchers tied natural enemy population dynamics to actual biocontrol services provided in less than half of the studies (Furlong & Zalucki 2010), and there has been growing concern about the lack of methodology tying cover crop use and natural enemy abundance to crop yields, especially in temperate systems (Gurr et al., 2017).

Cover cropping can provide habitat and food resources for natural enemies following crop harvest until the new growing season, or in the case of living mulches, enhance season long plant diversity. Cover cropping, therefore, has the potential to improve conditions for natural enemies by increasing vegetational diversity (Landis et al., 2000) and facilitating biological control service delivery (Blubaugh et al., 2016). Winter cover crops consistently show benefits in natural enemy communities and associated pest control in perennial systems (Gomez et al., 2018; Dong et al., 2018; Vogelweith & Thiery, 2017; Burgio et al., 2016). Yet, the response of natural enemies to cover crops and other habitat management strategies in row crop systems is highly variable (Daryanto et al., 2018; Begg et al., 2017; Tscharntke et al., 2016).

The resulting effect on natural enemies, pest, and production in annual systems often varies depending on the cropping system and cover crop species used. For example, Carabidae activity is increased in soybean plots containing a rye cover crop compared to plots without a cover (Dunbar et al., 2017). In a cereal and sown cover crop mosaic landscape, aphid parasitism is greater in areas close to sown mustard cover crops compared to areas with spontaneous non-crop plants (Damien et al., 2017), highlighting the advantage of selectively managing field and landscapes for biocontrol services as opposed to spontaneous non-crop vegetation alone. Additionally, a rye cover crop can reduce pest populations such as of aphids in soybeans (Koch et al., 2015), or thrips in multiple systems using various covers (Manadhar et al., 2017; Toews et al., 2010). However, cover crops sometimes negatively influence natural enemies or crop production. In a squash system, cover crops had no influence on the number of predators or herbivores found on squash plants, and the highest yields were achieved in control plots lacking a cover crop (Buchannan and Hooks, 2018). Similarly, the use of a cover crop significantly increased the abundance of imported cabbageworm pests when a rye cover crop was used in a cabbage system compared to no cover crop controls (Bryant et al., 2014). In other cases, there seems to be no discernable effect of cover crops on natural enemies or pest control services. For example, in a recent study by Lou et al. (2019), none of the cover crops assessed influenced arthropod diversity, evenness or pest pressure; however, they did show the potential advantages of using cover crops for other ecosystem services without negative effects on pest management or yield. Due to the variability in natural enemy responses to cover crops in different systems, there is a strong need to assess the mechanisms of natural enemy population build-up in response to cover crops, and assess how any changes in natural enemy communities correlate with pest control services.

Cotton

Cotton accounts for nearly 40% of fiber production worldwide and is one of the largest users of insecticides nationally (ERS, USDA 2014). Cotton production and pest management has changed significantly in recent years with the widespread adoption of transgenic cotton varieties targeting herbicide resistance and control of lepidopteran pests. Although pesticide inputs have decreased in cotton, they still account for over 7% of pesticide use in major U.S. Crops, and growers typically spend on average $65 per acre on applications (ERS, USDA 2014). Adoption of transgenic crops has reduced pesticide use, but has also led to increased agricultural intensification through the simplification of farming practices. This increased simplification allows growers to indiscriminately apply insecticides and herbicides targeting non-lepidopteran pests without concern for crop losses, further contributing to the “pesticide treadmill” typically associated with genetic uniformity and reductions in biodiversity (Garcia and Altieri 2005). Although the widespread adoption of transgenic Bt cotton in the US has reduced pesticide use on lepidopteran pests, it has created opportunities for previously benign pests to reach economically damaging levels. Subsequently, pest control in the southern US has shifted focus onto damage caused by early season thrips and a complex of late season heteropteran pests (Naranjo 2010).

The response to damage caused by these pests is application of pesticides early in the season for the control of thrips, and later in the season for stink bugs. Thrips are the most consistent insect pest of cotton in Georgia, and high levels of infestation by these pests have been shown to impede cotton development and reduce lint quality and yields (Greenberg et al., 2009). Current management practices for early season thrips focus on control through the use of preventative seed coat insecticides and broad spectrum foliar sprays after emergence. The reliance on pesticides has led to resistance in common thrips species, and several insecticides are more damaging to natural enemies of these pests (Bielza, 2008).

Thrips in the genus *Frankliniella* are a serious pest of seedling cotton as well as several other crops worldwide (Toews et al., 2010; Greenberg et al., 2009; Mouden et al., 2017). In previous studies, strip tillage and cover crops helped suppress early season thrips populations (Toews et al., 2010; Knight et al., 2017; Manandhar et al., 2017). Conversely, stink bugs, a mid-to-late season cotton pest, are challenging to control and force producers to rely on broad spectrum insecticides such as pyrethroids and organophosphates (Roberts & Toews, 2015), which are harmful to natural enemy communities (Gurr et al., 2017; Isaacs et al., 2009). There is building interest in management practices that reduce chemical inputs in favor of more environmentally friendly and sustainable options. Conservation biological control has been suggested as a promising pest management tactic for these and other pests of cotton (Bottrell and Adkisson 1977; Naranjo & Ellsworth 2009). Encouragingly, upwards of 300 species of predatory and parasitic arthropods are associated with cotton agroecosystems (Bottrell and Adkisson 1977). However, annual systems such as cotton are ephemeral, which reduces possibilities for conservation biological control due to disturbances (e.g. tillage and pesticides) and vegetation removal. Therefore, improving biodiversity in annual systems is dependent on promoting habitat within (Amaral et al., 2016) and around production fields (Landis et al., 2000; Gurr et al., 2017), and avoiding insecticides. Cover crops provide a unique opportunity for stable habitat in the off season and additional habitat complexity in field during the growing season.

Molecular Gut-Content Analysis (MGCA)

Understanding how habitat management influences the functions of arthropod communities in agroecosystems requires documenting species interactions. The function of predator communities is dependent of the interactions between predators and their prey, but understanding the complexity of trophic interactions in agroecosystems can be difficult (Greenstone & Sunderland 1999). Predator-prey interactions involving small and often cryptic invertebrate predators are difficult to track in field, especially using techniques such as direct observation or morphological identification of gut content (Sheppard et al., 2005). Furthermore, agricultural food webs include several fluid feeding predators making gut contents unidentifiable (Traugott et al., 2013), and are also largely composed of generalist predators (Symondson et al., 2002). Feeding habits of generalist predators are especially difficult to assess and are potentially influenced by a number of factors including: abundance of available prey, interference by other predators, and microhabitat availability in addition to several other abiotic factors (Symondson et al., 2002). Additionally, the prey breadth of predators can vary widely among taxa (Sheppard and Harwood 2005), as can hunting modes. Some predators such as many carabids are opportunistic omnivores, feeding on a range of both plants and animal material (Traugott et al., 2013). Although difficult, understanding these trophic relationships in agroecosystems can help to target beneficial predator communities and maximize biological control services.

Recent advances in tools for molecular ecology have allowed researchers to move from visual observations of predation and morphological analysis of gut contents to more effective and efficient methods of identifying trophic linkages. In recent years, Polymerase chain reaction (PCR) has become the most common way to assess prey presence in higher trophic levels (King et al., 2008; Traugott et al., 2013). Using multiplex PCR, predators can be screened for several prey items including pests and alternative prey. This is ideal when screening a large number of individuals for prey DNA (King et al., 2008), is highly sensitive, and cost-effective compared to other methods including stable isotope and fatty acid analysis (Traugott et al., 2013). Several studies have utilized PCR to begin understanding trophic networks in agricultural systems. Harwood et al. (2007) found that *Orius insidiosus* was a major predator in a soybean system contributing to the biological control of the soybean aphid, *A. glycines*. Kuusk and Ekbom (2012) used aphid and collembolan specific primers to determine how wolf spiders (Lycosidae) prey choice is affected by prey densities. Additionally, PCR has been used to determine how habitat complexity effects the predation frequency of generalist predators (Szendrei et al., 2010, 2014) and the frequency of intraguild predation among spiders and carabids (Davey et al., 2013; Roubinet et al., 2017). It is becoming clear that species do not interact in a vacuum, and it is increasing necessary to understand interactions between entire species assemblages in field settings to understand the realized effects of management strategies on the delivery of ecosystem services and crop production.

Research objectives and approach

1. Evaluate the effects of different cover crops on arthropods and cotton production
    a. Assess the abundance and diversity of arthropod natural enemies in response to 3 cover crop treatments (no cover, crimson clover, rye) at each manor cotton development stage

   b. Estimate pest pressure of both thrips (*Frankliniella* spp.) and southern green stink bug (*Nezara viridula)*, as well as stink bug egg predation in response to cover crop treatments
   c. Measure the effects of cover crops on cotton production including cost of cover crop management, cotton yield and fiber quality
2. Investigate how the use of different cover crops alters predator community composition and function throughout the cotton growing season
   a. Determine if the use of cover crops promote structurally dissimilar predator communities across the season.
   b. Assess the function of predatory communities by quantifying trophic interactions between predators, pests and non-pests using molecular gut content analysis
   c. Measure changes in function and stability of these communities by estimating changes in predator-prey interaction networks.
3. Provide resources to growers and extension professionals highlighting the importance of arthropod predators in Georgia cotton and the role they play in pest suppression.
   a. Identify common natural enemy species found in cotton production systems in the region as well as the most prevalent pests.
   b. Provide a resources with information concerning the identification, timing, and function of predators in Georgia cotton

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CHAPTER 2

COVER CROPS IMPROVE EARLY SEASON NATURAL ENEMY RECRUITMENT AND PEST MANAGEMENT IN COTTON PRODUCTION

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Abstract

A shift to more ecologically based farming practices would improve the sustainability and economic stability of agricultural systems. Habitat management in and around agricultural fields can provide stable environments that aid in the proliferation of natural enemy communities that moderate pest populations and injury. Winter cover crops offer a potentially cost-effective approach to improving habitat that supports natural enemy communities early in the growing season. We investigated the effects of winter cover crops including cereal rye (*Secale cereal* L.) and crimson clover (*Trifolium incarnatum* L.) on the abundance and diversity of natural enemies, key pest populations, biological control services, and cotton yield. Winter cover crops were established on 0.4 ha replicated field plots in the fall of 2017 and 2018. Suction sampling during each cotton development stage demonstrated that a rye cover crop promoted greater abundance and diversity of natural enemy communities in early cotton stages. Extensive leaf sampling of seedling cotton showed that cover crops significantly reduced thrips infestations. Furthermore, stink bug boll injury decreased on plots prepared with a rye cover compared to cotton lacking this additional habitat. Combining end of season yield results and management practices with an economic analysis of the costs of production, the value of cotton grown into a cover crop was cost competitive with conventional (no cover) cotton production. These results suggest that conventional growers utilizing cover crops could reduce insecticide inputs through natural reductions in pest pressure, and overall do not incur additional production costs.

Keywords: cover crops, habitat management, natural enemies, thrips, stinkbugs, cotton, crop development stage, conservation

Introduction

Meeting food and fiber demands of a growing population is often focused on increasingly intensive agricultural practices including synthetic fertilizers and pesticide applications (Matson et al., 1997; Fedoroff et al., 2010; Tilman et al., 2011). Although these intensive practices can support high levels of production, there are recognized negative environmental trade-offs to biodiversity (Tscharntke et al., 2005; Landis, 2017; Wittwer et al., 2017), water quality (Matson et al., 1997), and soil health (Stavi & Lal, 2015). Balancing reliance on synthetic inputs with biologically based, ecosystem services (e.g. biological control, pollination, nutrient cycling), is advocated to promote environmentally friendly solutions for the challenge of feeding a growing population (Rusch et al., 2017; Wittwer et al., 2017; Murrell, 2017; Kaye & Quemada, 2017; Tilman et al., 2011; Landis, 2017). This shift, known as ecological intensification, can improve the long-term sustainability and ecological stability of agricultural ecosystems.

Promoting ecosystem services can be achieved through improving conservation practices that favor local biodiversity combined with reduction in broad spectrum insecticides (Shields et al., 2018; Snyder, 2019, Gurr et al., 2017; Begg et al., 2017; Gurr et al., 2000, Landis et al., 2000). For example, managing the habitat in and around agricultural fields can mitigate some effects of intensive management to increase the effectiveness of natural enemies by promoting more abundant and diverse predator communities (Gurr et al., 2017). A variety of mechanisms are proposed for the effects of habitat management on predator communities, including: provisioning of alternative prey, and minimizing intraguild predation via additional microhabitat availability (Finke & Denno, 2002; Janssen et al., 2007). Habitat fueling alternative prey availability helps sustain natural enemy populations during periods when there is little to no crop habitat (Staudacher et al., 2018; Gardarin et al., 2018; Roubinet et al., 2017). Thus, efforts to promote habitat diversity may create a “resource bridge” to build diverse natural enemy communities ready for invading pests.

Winter cover crops are a form of habitat management that adds habitat complexity into cropping systems, and enhances multiple ecosystem services critical to sustainable crop production (Daryanto et al., 2018; Duzy & Kornecki, 2017; Adhikari et al., 2017). Cover crops are often planted to suppress weeds and reduce erosion, and provide several additional benefits such as improving soil health by fixing nitrogen, sequestering excess soil nutrients (Hartwig &Ammon, 2002), or sequestering atmospheric carbon and building soil organic matter (Kaye & Quemada, 2017). Additionally, cover crops and in field cover crop residue provide habitat diversity, which may improve natural pest control services by increasing the abundance and effectiveness of natural enemies in field.

Winter cover crops often benefit natural enemy communities and pest control in perennial systems (Gomez et al., 2018; Dong et al., 2018; Vogelweith & Thiery, 2017; Burgio et al., 2016). Yet, the response of natural enemies to cover crops and other habitat management strategies in row crop systems is variable (Daryanto et al., 2018; Begg et al., 2017; Tscharntke et al., 2016). In annual row crop systems, positive effects of cover crops on natural pest management appear driven by a combination of cropping system, geographical region, and cover crop type (Hooks et al., 2013; Mollot et al., 2012; Koch et al., 2015; Manandhar et al., 2017). Hence, there is a need for system and region specific studies examining the impact of cover crops on natural enemy communities and pest complexes. Additionally, few studies link changes in predator abundance and diversity to increased biological control services (Furlong & Zalucki, 2010), and for cover cropping to be fully integrated into the pest control tool box, any benefits must be linked to production value (Gurr et al., 2017).

Current insect pest management programs and pesticide usage for cotton in the southeastern United States are focused on early season thrips and a complex of late season stink bugs (Tillman, 2012; Lahiri et al. 2018). Thrips in the genus *Frankliniella* are a serious pest of seedling cotton as well as several other crops worldwide (Toews et al., 2010; Greenberg et al. 2009; Mouden et al. 2017). In previous studies, strip tillage and cover crops helped suppress early season thrips populations (Toews et al., 2010; Knight et al. 2017; Manandhar et al., 2017). Conversely, stink bugs, a mid-to-late season cotton pest, are challenging to control and force producers to rely on broad spectrum insecticides such as pyrethroids and organophosphates (Roberts & Toews, 2015), which are harmful to natural enemy communities (Gurr et al., 2017; Isaacs et al., 2009). There is building interest in management practices that reduce chemical inputs in favor of more environmentally friendly and sustainable options.

In this study, we investigated the effects of winter cover crops including cereal rye (*Secale cereal* L.) and crimson clover (*Trifolium incarnatum* L.) on the abundance and diversity of natural enemies, key pest populations, biological control services, and cotton productivity. We hypothesized that (1) the presence of cover crop residue increases the abundance and diversity of natural enemies, (2) the presence of a cover crop reduces numbers of early season thrips and late season stink bug pests, (3) cover crops improve biological service delivery on sting bugs by indirectly increasing predation on stink bug eggs, and (4) cover crops have positive effects on end of season production.

Materials and Methods

Study Site and Experimental Design. We investigated the effects of cover crops in a Georgia cotton production system by establishing plots in the fall of 2016 and 2017 at the UGA Southeast

Georgia Research and Education Center at Midville, GA (Burke County, 32°52'15.6"N 82°13'12.0"W). The experimental design consisted of 0.4 ha plots (roughly square) organized in a completely randomized block design (n=4/treatment) for a total of 12 plots each sample year. All plots were separated by 3.6 m rolled rye alleyways. A control (no cover) was maintained throughout the off-season and managed following conventional tillage and winter herbicide applications common to southeast cotton production (Appendix A.1). Crimson clover (27 kg/ha) and rye (67 kg/ha) cover crops were planted early November using a cultipacker or grain drill and chemically terminated and rolled using a straight bar roller crimper 14 days prior to cotton planting. Cotton was planted into cover treatments May 5, 2017 (PHY 490 W3FE) and April 28, 2018 (PHY 440 W3FE) using a Unverferth strip till rig leaving an 8-inch tilled strip to serve as a seed bed, while conventionally tilled plots were disked followed by a rip and bed pass. All fields were irrigated during cover crop growth and the cotton growing season, and received no insecticides throughout the study (for full plot management details see Appendix A.1, A.2).

Arthropod Sampling. Canopy and ground dwelling arthropods were sampled using a 27.2cc modified reverse-flow leaf blower (SH 86 C-E; Stihl, Waiblingen, Germany) containing an average air velocity of 63 m/s with a mesh bag over the intake to collect natural enemies within a 1 m^2 area quadrat. These areas within each plot were delineated by placing a 1 m^2 quadrat, custom fabricated from 0.48 cm thick clear acrylic sheet with 0.3 m tall walls and metal bottoms, on the soil surface to prevent escape by ground dwelling or low-flying arthropods. Actual sampling locations were randomly selected on each sample date and all samples were at minimum 10 m from the plot edge (3 samples per plot). All cotton plants and cover crop residue within the 1 m^2 area was suctioned (~1 min/sample) until there was no visual arthropod activity on the ground or in the canopy after visual inspection. Suction sampling occurred during each of the primary cotton development stages (pre-emergence, seedling, vegetative growth, squaring, flowering, boll development), for a total of 6 sampling dates per plot during the 2017 and 2018 cotton growing seasons (Appendix A.3). All samples were placed in plastic bags and immediately stored in on ice, and preserved at -20° C until identification. All arthropods were identified to the family level with adult natural enemies identified to genus and species, when possible.

Adult and nymph thrips (Thysanoptera: Thripidae) populations were assessed in every plot during seedling growth stages at 14 and 21 days after cotton planting following standard protocols (Toews et al., 2010). On each date, two samples of 5 plants were randomly collected in a diagonal transect (across rows) starting at least 10m from field margins. Briefly, whole cotton seedlings were removed from the soil and immediately inverted in 0.47 L glass jars (5 plants/jar) partially filled with 70% ethanol where the plants were vigorously agitated to dislodge thrips. In the laboratory, the alcohol was passed through a 125 μm sieve and the thrips were retained on the sieve and then gently washed onto gridded filter paper, identified and enumerated under a dissecting microscope.

Stink bug pressure was evaluated during cotton anthesis using sweep nets and boll injury assessments (following protocols by Toews et al., 2008). The primary stink bug complex in the southeast cotton cropping region is made up of the southern green stink bug, *Nezara viridula* L., the green stink bug, *Acrosternum hilare* Say, and the brown stink bug, *Euschistus servus* Say. Two sweep net samples (20 sweeps/transect) were performed in each plot (one at 20 m from one edge of the plot and at a parallel location on the other side of the plot) and the number of stink bugs was recorded. Stink bug species and life stage were recorded and the combined count of all non-predatory stink bugs was used for analysis (Appendix A.4). For evaluation of feeding damage on cotton bolls, 2.3 to 2.7 cm diameter bolls (Willrich et al., 2004) were collected from the same two transects in each plot and checked for symptoms of stink bug feeding (20 bolls/plot for 2017, 40/ plot for 2018). Internal boll injury was defined by the presence of callus growths (warts) or stained lint (Greene et al., 1999, Bundy et al., 2000), with bolls classified as injured or uninjured. Stink bug sweeps and boll collection starting at the 2nd week of bloom were performed for 4 weeks, once per week during the cotton anthesis.

Estimating Biocontrol Services. To evaluate biocontrol services provided by natural enemies, egg predation and parasitism were estimated from sentinel egg masses. At the beginning of 2017 and 2018 cotton seasons, *Nezara viridula* colonies were established from field collected adults, and maintained to produce stink bug egg masses. Egg masses (3-5 day old) were collected from the colony one day prior to field deployment and stored in a refrigerator at 4-8 ° C. Colony egg masses laid on paper towels were cut to remove excess paper material and stapled to a 3.0 x 3.5 cm index card. Egg masses were affixed to 4 cotton plants per plot during the cotton flowering period for a total of 3 dates in 2017 and 4 dates in 2018. Egg masses were attached to plants on the underside of a main stem leaf at the first node above white flower. Plants were selected in a square (5 x 5 m) around the center of the plot, and marked with colored tape for easy detection and retrieval. After a 48-hour period, egg masses were collected and transported to the lab where the number of eggs missing or damaged was used to assess mean predation rates (percent egg removal). All egg masses were photographed before they were placed in the field and after collection. Remaining eggs were incubated and monitored for emergence of parasitoids to estimate egg parasitism rates.

Cover Crop Biomass and End of Season Yield/Fiber Quality. During the 2018 season, live cover crop biomass was estimated prior to cotton planting. All above ground cover crop biomass within a 0.3 m^2 area was clipped at the soil surface and collected (excluding conventionally managed plots), and three samples were collected from each plot. Collected samples were stored in paper bags and dried for 48 hours in a gravity convection oven at approximately 60 °C and dry weight recorded for each sample.

End of season cotton yield and fiber quality were estimated for both years by harvesting along two 24 m transects per plot using a mechanized two row spindle picker. Following harvest, seed cotton was weighed and then ginned on a per sample basis at the University of Georgia Cotton Micro Gin in Tifton, Ga to determine lint and seed fractions. Samples of lint were submitted to the Cotton Program Classing Office in Macon, GA to determine any differences in fiber quality.

To estimate the economic benefits of adopting cover crops in cotton production, the net return per acre was compared for each of the three treatments of cover crops (i) for 2017 and 2018 (t). The gross revenue was calculated using the lint and cottonseed yields and their historical prices each year.

$$Gross\ revenue_{i,t} = lint\ price_t \times lint\ yield_{i,t} + cottonseed\ price_t \times cottonseed\ yield_{i,t}$$

The prices for cotton lint include the cotton loan price and market price to compare the effect of prices on the profitability of different treatments. Cotton loan price is the minimum amount of money farmers would receive for their cotton with specific fiber quality. Market price for cotton lint were calculated from incorporating fiber quality by using the annual cotton price statistics from U.S. Department of Agriculture, Agricultural Marketing Service (USDA-NASS 2018). Costs were calculated based on the input uses and farming practices in planting cover crops, cultivating the land, planting cotton, herbicide applications, harvesting and ginning of cotton (for additional details of analysis see Appendix A.7). The cost was calculated using the following equation:

$$Cost_{i,t} = field\ preparation\ costs_{i,t} + costs\ for\ planting\ cover\ crop_{i,t} + costs\ for\ planting\ cotton_{i,t} + herbicide\ and\ application\ costs_{i,t} + harvesting\ and\ ginning\ costs_{i,t}$$

The net return per acre for cotton production was calculated for each of the treatment and each production season as follows:

$$Net\ retun_{i,t} = gross\ revenue_{i,t} - total\ cost_{i,t}$$

Data Analysis. Due to inter-annual variability, response variables were analyzed and displayed separately for 2017 and 2018. Predator density (number per m^2) and Shannon diversity (H) were calculated for each sample throughout the growing season. Square root transformations for all count responses were required to normalize distributions and satisfy model adequacy. Predator density and diversity, stink bug and thrips abundance in relation to cover cropping treatments were analyzed using linear mixed effect models (LMM) (function = lmer, package = lme4; Bates et al., 2014) with date as a fixed effect, and plot as a random effect to account for repeated measures of plots over time. Production metrics were only estimated for the end of season, so a basic ANOVA model was used to compare production (i.e. yield, fiber quality, etc.; Table 1) between cover crop treatments. To test for significant effects of LMMs and ANOVAs, contrasts were evaluated at the 95% confidence interval with adjusted p-values for multiple comparisons using the “Tukey” method (function=lsmeans, contrast; package = lsmeans, Luke, 2017). Cumulative egg predation and proportion of injured bolls were evaluated in relation to cover crop treatments using generalized linear mixed-effect models (GLMM) for analysis of proportions (function = glmer, package = lme4) using plot and date as nested random effects (family=binomial). For significant effects of GLMMs, contrasts were evaluated at the 95% confidence interval with p-values adjusted using the "holm" method (function=glht, contrast; package = lsmeans, Luke, 2017). All statistical analyses were performed in R v 3.3.2 (R Core Team, 2018).

Results

Natural enemies. A total of 2,675 predators were collected during the 2017 (1,123) and 2018 (1,552) sampling seasons (Appendix A.5). In 2017, predator density was significantly influenced by cover crop treatment (LMM: $F_{2,12}=3.90$, $p=0.049$) and sampling date (LMM: $F_{5,216}=33.15$, $p<0.0001$) with a significant interaction between cover crop treatment and date (LMM: $F_{10, 216}=8.41$; $p<0.0001$; Fig 2.1). Likewise, in 2018 predator density was significantly influenced by treatment (LMM: $F_{2,217}=46.32$, $p<0.0001$), date (LMM: $F_{5,217}=14.92$, $p<0.0001$) and an interaction between treatment and sample date (LMM: $F_{10, 217}=10.30$; $p<0.0001$; Fig 2.1). In the interaction between date and cover crop treatment indicates differences in predator density and diversity in the early growing season in both years in relation to cover crops (Fig 2.1; Appendix A.6). In 2017, a rye cover crop harbored significantly higher densities of natural enemies than no-cover conventional plots prior to seedling emergence (Fig 2.1). In 2018, a rye cover crop significantly improved predator density through seedling stage of cotton, while crimson clover showed no improvement over no-cover treatments (Fig 2.1; Appendix A.6).

Similarly, we observed a significant effect of cover crop treatment (LMM: $F_{2,9}=8.58$, $p=0.0081$), date (LMM: $F_{5,201}=26.32$, $p<0.0001$) and a treatment by date interaction (LMM: $F_{10, 201}=5.65$; $p<0.0001$; Fig 2.1) in explaining diversity (H) of natural enemies in 2017. Similar effects of treatment (LMM: $F_{2,199}=8.69$, $p=0.0002$), date (LMM: $F_{5,199}=26.22$, $p<0.0001$) and treatment by date interaction (LMM: $F_{10,\,199}$=3.32; p=0.0005; Fig 2.1) on natural enemy diversity were found in 2018. In 2017, the rye cover crop elevated predator diversity through the leafy growth stage of cotton compared to no-cover plots (Fig 2.1; Appendix A.6). In 2018, rye maintained significantly higher diversity of predators through the seedling stage compared to conventionally management plots (Appendix A.6).

Thrips. Due to low thrips pressure, no assessment on thrips populations were feasible for the 2017 growing season (i.e. not detectible across all treatments). For 2018, the total number of thrips varied by sample date (LMM: $F_{1,\,32}$=122.7; p<0.0001), with a greater abundance of total thrips 21 days after planting (DAP) compared to 14 DAP (Fig 2.2). The abundance of thrips adults was influenced by date (LMM: $F_{1,32}$=120.33, p<0.0001), with a significant interaction between treatment and date (LMM: $F_{2,\,32}$=32.2; p=0.004). The interaction for adult thrips is explained by the fact that abundance was marginally affected by cover crop treatment 14 days after planting (Fig 2.2), though we found no difference in adult thrips abundance among treatments at 21 DAP. Nymphal thrips abundance was significantly influenced by treatment (LMM: $F_{1,\,9}$=5.54; p=0.027), date (LMM: $F_{1,\,32}$=21.05; p<0.0001) and an interaction between treatment and date (LMM: $F_{1,\,32}$=3.77; p=0.034). Rye and crimson clover cover treatments had significantly lower abundance of thrips nymphs on cotton seedlings compared to the no cover treatment 21 days after cotton planting (Fig 2.2), with no difference among treatments 14 days after planting.

Stink Bugs. The effect of cover crop treatments on stink bug abundance and boll injury was assessed during both sample years. The most common stink bug species collected in sweep samples was *N. viridula*, making up 84% of all stink bugs sampled in 2017, and 38% in 2018 (Appendix A.4). There was no effect of cover crop or date on stink bug abundance in field during either year, though boll injury has been suggested as more accurate indicator of stink bug pressure than total or mean abundance (Reay-Jones et al., 2010; Toews et al., 2010). A total of 2,639 bolls were assessed for stink bug feeding injury over 2 years. There was no effect of cover crop treatment on the proportion of cotton bolls injured in 2017 (GLMM: $\chi^2_{2,31} = 1.35$; p=0.509). However, cover crop treatment significantly influenced the proportion of bolls injured in 2018 (GLMM: $\chi^2_{2,43} = 11.33$; p=0.040; Fig 2.3). Overall stink bug pressure was much higher during the 2018 season than in 2017, and boll injury was significantly lower in rye plots compared to conventionally managed no-cover plots (Fig 2.3).

Biological control services. Across both sample years, 336 *N. viridula* sentinel egg masses were placed in the field to estimate predation and parasitism rates. We found no effect of treatment on rates of egg predation in either 2017 (GLMM: $\chi^2_{2,33} = 1.35$; p=0.51) or 2018 (GLMM: $\chi^2_{2,45} = 2.21$; p=0.33). All emerging parasitoids were identified as *Trissolcus basalis*. Parasitism of southern green stink bug egg masses was very low for both sample years (0.05% in 2017 and 0.02% in 2018).

Cover crop biomass and cotton production. Cover crop biomass samples were used to evaluate the establishment and coverage of each cover crop treatment. Rye cover crops provided significantly higher initial biomass compared to crimson clover (Table 2.1). At the end of each growing season, yield and fiber quality were assessed to determine the effects of cover cropping treatments on cotton production. There was no effect of cover crop treatment on end of season cotton lint or seed yield alone, yet some aspects of cotton fiber quality were significantly influenced by cover crop treatment (Table 2.1; Appendix A.8). Net return at both loan value and market value, including total cost of cover management, did not differ significantly among management treatments in 2017 (ANOVA_{loan}: $F_{2,9}$=0.93, p=0.430; ANOVA_{mkt}: $F_{2,9}$=0.29,

p=0.753) or 2018 (ANOVA$_{loan}$: $F_{2,9}$=1.27, p=0.326; ANOVA$_{mkt}$: $F_{2,9}$=1.70, p=0.231; Fig 2.4). Both loan value (ANOVA: $F_{1,24}$ = 54.80; p<0.0001) and market value (ANOVA: $F_{1,24}$ = 8.62; p = 0.007) of cotton produced was greater in 2017 compared to 2018, independent of cover crop treatment (Fig 2.4). For further details regarding cotton premiums and commodity value by treatment, see supplementary materials (Appendix A.8).

Discussion

Winter cover crops provide multiple ecosystem services to agricultural systems (Hartwig & Ammon, 2002; Daryanto et al., 2018; Duzy & Kornecki, 2017; Adhikari et al., 2017). There is currently unharnessed potential of using cover crops to improve crop protection and reduce chemical inputs in annual production systems such as cotton. Our results supported aspects of our hypotheses by providing evidence of early season reduction in pest pressure, and correspondingly higher density and diversity of natural enemies. Importantly, our study demonstrates that integrating cover crops into the cotton production system results in similar costs of production and equivalent yields and quality of fiber produced.

Rye was more effective than either crimson clover or the no cover treatments at promoting higher natural enemy density and diversity. Differences in predator responses to cover crop treatments may be attributed to the type, and quality of resources provided by the cover crop, but also cover crop biomass. Quantity of cover crop residue influences weed suppression and other ecosystem services provided by cover crops (Toler et al., 2019; Finney et al., 2016; MacLaren et al., 2019). Thus, the significantly improved initial biomass of the rye cover crop (Table 2.1) may explain its increased effectiveness in promoting and harboring a high density and diversity of natural enemies. Increasing plant diversity is shown to increase the availability and diversity of herbivores (Siemann et al., 1998; Welti et al., 2017), which serve as prey when crop habitat is minimal in the early season (Moreira et al., 2016). The addition of habitat complexity to agricultural systems also correlates with prey consumption by generalist natural enemies through provisioning of alternative food sources (Staudacher et al., 2018). Our findings of increased natural enemy density in cover crops is consistent with previous literature focusing on predator response to habitat manipulations that improve the quality or quantity of habitat in an agroecosystem (Ribeiro & Gontijo, 2017; Depalo et al., 2017; Letourneau et al., 2011; Andow, 1991; Gurr et al., 2000; Holland et al., 2012). Therefore, we show that cover crops, especially rye, are an effective means of bolstering natural enemy communities ready to respond to pest immigration (i.e. early season thrips).

Cover crops provided notable suppression of early season thrips pests, with particularly low numbers of thrips nymphs found in rye in a majority of samples (Fig 2.2). Adult thrips are winged and mobile and their number and distribution in field indicate where thrips are present and active. Thrips nymphs are wingless and are unable to move between plots, therefore number of thrips nymphs is an effective estimate of thrips development and feeding pressure on seedling cotton. Our results suggest that the presence of a cover crop had a significant positive effect on early season thrips control compared to our conventional management treatment (Fig 2.2), particularly the pressure and development of nymphal thrips on cotton. While we lack a direct test of the link between improved predator density and lower thrips counts, we did observe both higher numbers of predators and higher diversity, and lower numbers of thrips developing on cotton. Further research is needed to test proposed mechanisms and competing hypotheses for early season thrips response to cover crop use and habitat complexity (González-Chang et al., 2019; Brévault & Clouvel, 2019). Previous studies in cotton have found similarly reduced thrips pressure in cover cropped plots (Toews et al., 2010; Olson et al., 2006) suggesting that cover crops can provide a measure of thrips control without an in-furrow or foliar insecticide application.

Additionally, cover crops can provide relief from pest pressure into the late season, despite the similarities in the abundance and diversity of predators among treatments (Fig 2.1). Our results indicate that when stink bug pressure is low, boll injury was similar across treatments. However, our results suggest that in years with high stink bug pressure, cover crops reduce levels of stink bug damage as much as 10% when compared to conventional management practices (Fig 2.3). Predation and parasitism of stink bug eggs has been shown provide a measure of control of pests in the field (Tillman, 2011), although we found no link between cover crop treatment and enhanced late season predator communities or the predation of *N. viridula* eggs (Fig 2.3). Regardless of the exact mechanism, we show that cover crops can provide relief from high stink bug pressure, reducing the injury on developing bolls and potentially mitigating the impact on cotton production. Stink bug feeding and injury can have significant effects on cotton yield and quality, through direct damage of cotton seeds and lint resulting in abortion of young bolls, lint discoloration, and reduced lint production (Wene & Sheets, 1964; Barbour et al., 1988; Roach, 1988). Furthermore, feeding by *N. viridula* can result in the introduction of microorganisms resulting in boll rot (Willrich et al., 2004) or bacterial pathogens which affect boll development (Medrano et al., 2007), making evaluation of both end of season lint yield and quality important for determining the overall effect of cover crops and pest pressure on cotton production.

One of the primary concerns with the use of cover crops and strip tillage is the yield gap between conservation practices and conventionally managed cash crops (Ponisio et al., 2015;

Reganold & Wachter, 2016; Tilman et al., 2011). Here we show production costs and net return when using cover crops are competitive with common conventional production methods. Production value calculations used in this study provide estimates for the value of cover crops on production cost and maintenance over two years, although several studies have highlighted additional long-term benefits of cover crop use (Reeves, 2018; Daryanto et al., 2018; Poeplau & Don, 2015). Some recent studies indicated that using cover crops may reduce inorganic fertilizer demand (Mahama et al., 2016; Plaza-Bonilla et al., 2017; Wilson et al., 2019), and in the current study we held all inputs constant across treatments. Further consideration for reduced pesticide applications for weeds and insect pests will enhance our estimates of overall costs.

In closing, our study indicates positive effects of cover crops on natural enemy communities, and possible applications of cover crops to improve biological control as part of integrated pest management programs. We highlight the seasonal aspect of cover cropping benefits on biodiversity and biological control, showing strong early season effects on predator communities and reductions of pest pressure into the late season. We provide evidence to support the use of cover crops to improve the sustainability of current agricultural systems by reducing the need for synthetic inputs while maintaining competitive levels of production and promoting local biodiversity. Although relationships between cover crops, density and diversity of predators, and pest pressure are evident, further research is needed in guiding pest management thresholds and inputs into the system in relation to cover cropping system used and quality of the cover crop. Lastly, research demonstrates that native predators are particularly important in cotton production (Naranjo 2018), and the effectiveness of predator diversity in providing biological control is closely linked to the composition and function of predators in the field

(Heimpel & Mils, 2017); therefore, our future work will untangle how management strategies influence the composition and functional roles of native predators in cotton systems.

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Table 2.1. Mean (±SE) end of season cotton production metrics for 2017 and 2018, by treatment. Results of ANOVA are shown. Different letters within rows indicate significant differences among means. Significant P values (α<0.05) are in bold. Fiber quality metrics used as response variables include lint yield (kg/ha), color grade, staple (length in 32nds of an inch), micronaire (mic), strength (grams/tex), reflectance (Rd), yellowness (+B), HVI length (inches), and uniformity. Few provide full descriptions of fiber quality metrics in supplemental material (Table C.3).

2017	**No cover**	**Crimson clover**	**Rye**	**F**	**df**	**P**
Lint Yield kg/ha	985.03(40.9)	1005.78(70.87)	1033.25(27.24)	0.24	2,21	0.792
Color grade	29.75(1.25)	26.00(1.89)	27.25(1.83)	1.29	2,21	0.296
Staple	35.75(.16)	36.25(.25)	36.38(.26)	2.07	2,21	0.151
mic	4.15(.08)	4.25(.05)	4.35(.03)	3.36	2,21	0.054
Strength	32.78(.36)	33.05(.24)	33.81 (.26)	3.35	2,21	0.055
Rd	78.98(.27)^{a}	79.98(.26)^{b}	79.93(.33)^{b}	3.83	2,21	**0.038**
+B	8.03(.09)	7.95(.08)	7.78(.06)	2.74	2,21	0.088
HVI Length	1.11(.00)	1.13(.01)	1.13(.01)	2.30	2,21	0.125
Uniformity	82.88(.22)^{a}	83.23(.22)^{ab}	83.76 (.23)^{b}	4.01	2,21	**0.033**
2018	**No cover**	**Crimson clover**	**Rye**	**F**	**df**	**P**
Live cover biomass(g)	NA	2.50(0.69)^{a}	48.14(5.86)^{b}	59.83	1,22	**0.001**
Lint Yield kg/ha	929.49(48.07)	1033.85(54.58)	849.14(61.98)	2.82	2,21	0.082
Color grade	36.38(2.03)	34.88(1.89)	34.75(1.83)	0.22	2,21	0.803
Staple	37.63(.18)^{ab}	37.75(.25)^{a}	37.00(.19)^{b}	3.68	2,21	**0.043**
mic	3.71(.09)	3.83(.09)	4.00(.07)	3.19	2,21	0.061
Strength	31.75(.28)	31.99(.39)	31.69(.39)	0.19	2,21	0.825
Rd	74.39(.67)	75.10(.92)	76.36(.38)	2.09	2,21	0.149
+B	8.78(.11)^{a}	8.63(.11)^{ab}	8.4(.07)^{b}	3.72	2,21	**0.041**
HVI Length	1.17(.01)^{ab}	1.19(.01)^{a}	1.16(.01)^{b}	3.53	2,21	**0.048**
Uniformity	81.24(.16)	81.08(.29)	81.86(.24)	3.15	2,21	0.064

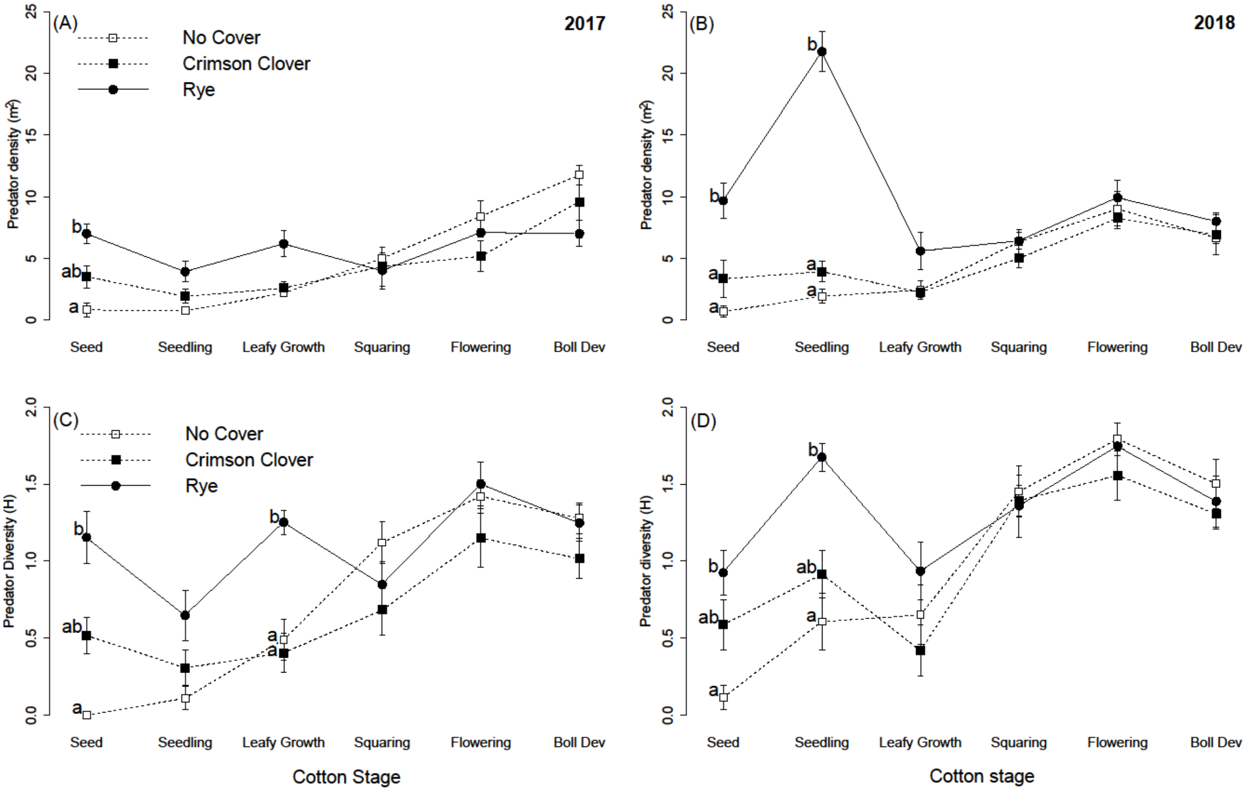

Fig. 2.1. Predator density (no. predators per m^2) (top panels A,B) and family level predator diversity (H) (bottom panels C,D) for the 2017 (left) and 2018 (right) sampling season across each major cotton development stage. Bars represent 1 SE of the mean for each treatment on each sample date. Letters indicate significant differences (α<0.05) among treatments on the same cotton development stage within years.

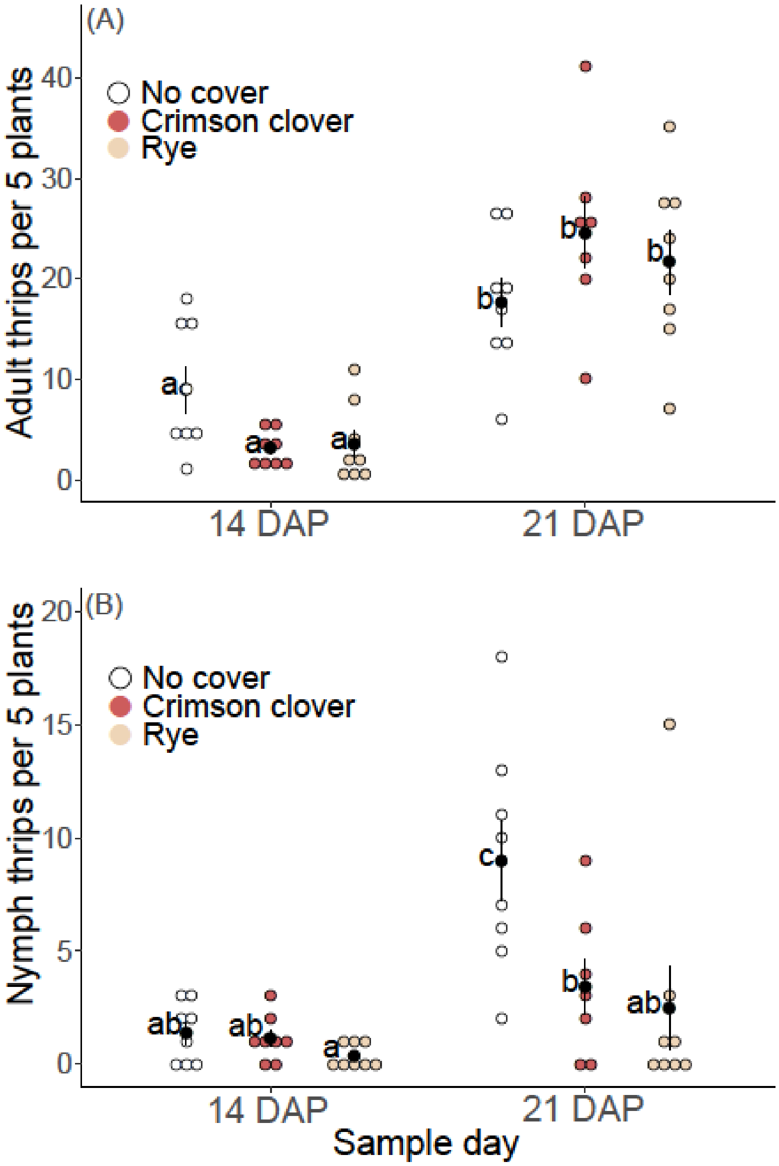

Fig. 2.2. Number of adult (A) and nymph (B) thrips per 5 plants 14 and 21 days after cotton planting (DAP) in Rye, Crimson Clover, and No-cover treatments. Black dots and error bars represent mean and SE. Letters next to dots indicate significant differences (α<0.05) in thrips of the same life stage among treatments.

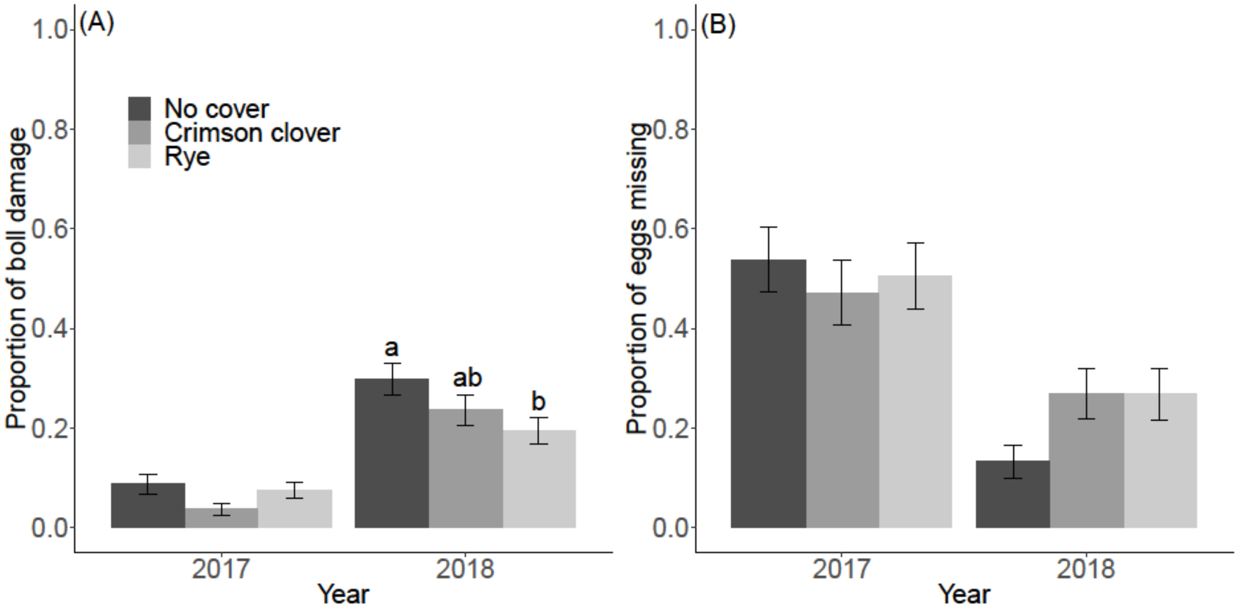

Fig. 2.3. Boll injury from stink bug feeding (A) and *Nezara viridula* sentinel egg predation (B) shown for each cover crop treatment in 2017 and 2018. Y axes are proportion ranging between 0-1, with high proportion of bolls injured indicating higher pest pressure, and increased proportion of eggs missing indicating higher egg predation. Letters indicate significant differences among treatments in the same year ($\alpha<0.05$).

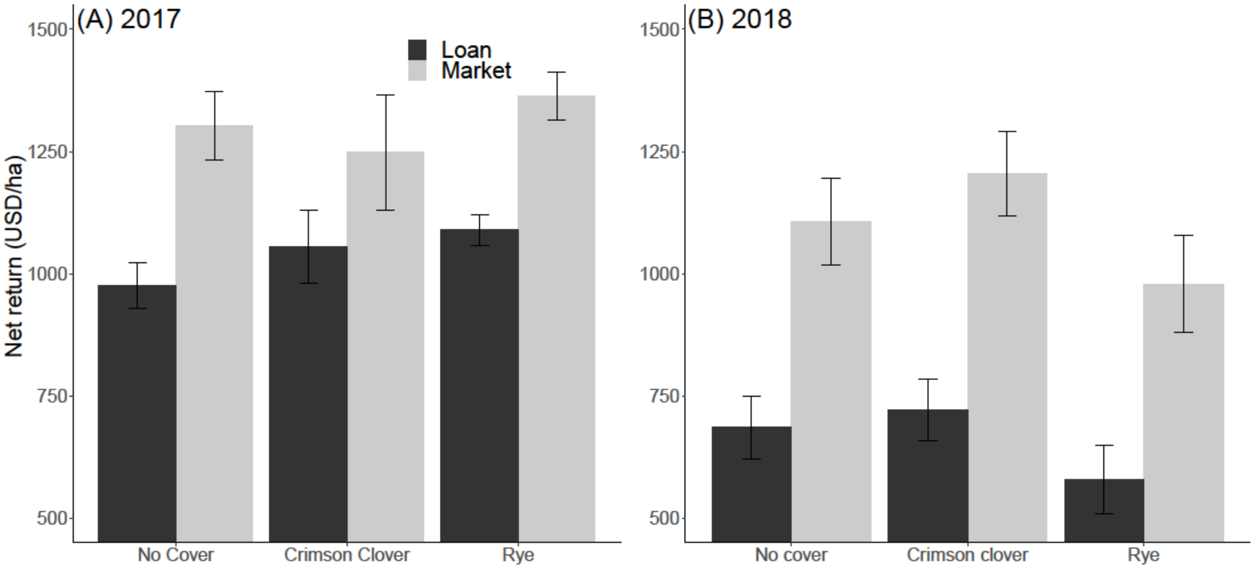

Fig. 2.4. Mean net return on harvested cotton per hectare at both loan value and market value for each treatment in 2017 (A) and 2018 (B) with error bars showing SE of the mean. Net return (USD/ha) includes total production and management cost of cover crop establishment and termination, as well management costs associated with conventional cotton production with no cover crop.

CHAPTER 3

LINKING HABITAT AND PREDATOR COMMUNITY FUNCTION THROUGH TIME: UNRAVELING THE TROPHIC EFFECTS OF COVER CROPS

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Abstract

Maintaining habitat throughout the season in annual cropping systems can provide resource stability for natural enemy communities when crop habitat is low. Increased resource availability potentially leads to stable arthropod communities and service provisioning by predatory arthropods in the form of biological control. There is a need for studies which identify mechanisms of predator community change due to habitat provisioning, and quantify community-level predation of economically important species. Here we use molecular gut content analysis to investigate the response of predator communities and interaction networks to rye and crimson clover cover crop use in a cotton system. Predators were collected from the field during each major cotton development stage in 2017 and 2018, and PCR was used to screen predators for the presence of primary cotton pests, incidental pests, and alternative prey. Cotton planted into cover crop residue promoted unique predator communities in the early and mid-season as compared to cotton planted in bare soil, with correspondingly dissimilar prey consumption among cover crop treatments. Temporal dynamics were observed in predator communities and their interactions with prey, with network characteristics indicating higher stability in the late growing season. We identify limitations for biological control of some key pests in this system and discuss potential mechanisms for altered predator communities and their function in the early season. We show that the use of winter cover crops can reduce the risk of early pest outbreaks by encouraging stable predator communities when there is little cotton habitat available.

Keywords: temporal patterns, habitat structure, cover crops, trophic interactions, arthropod communities, biodiversity – ecosystem function

Introduction

Annual agricultural systems experience dynamic cycles of vegetation growth and removal, affecting the prevalence and distribution of higher trophic level species (Wardle et al., 1999; Hanson et al., 2017; Bertrand et al., 2016). Establishing winter habitat in annual systems provides spatial refuges in periods of scarcity that support prey and non-prey resources needed by predatory arthropods (Blüthgen et al., 2016; Haro and Silveira, 2018). In particular, increasing diversity of plant communities often results in a corresponding increase in the abundance and diversity of predators (Letourneau et al., 2011, Moreira et al., 2016; Ebeling et al., 2018) and is thought to be correlated with the delivery of ecosystem services such as biological control (Gurr et al., 2017; Landis, 2017; Snyder, 2019). Alignment of natural enemy productivity with pest infestations is key to effective pest control, yet few studies investigate how the functional roles of natural enemies change across the growing season (but see Staudacher et al., 2018; Roubinet et al., 2018).

How biological control function is altered in response to increases in biodiversity depends on predator feeding traits and how species interact (Synder 2019; Schmitz, 2007). Additive or synergistic feeding behavior can improve pest suppression in diverse communities (Altieri, 1999; Cardinale et al., 2003; Wilby et al., 2005; Symondson et al., 2002). Yet, elevated diversity may hinder service delivery by increasing negative interactions between beneficial species (Janssen et al., 2007; Symondson et al., 2002; Tixier et al., 2013) or through increasing the availability of preferred non-pest prey (Koss and Snyder 2005; Holt and Huxel, 2007; Maselou et al., 2018). Consequently, simply improving diversity in agricultural systems is often not sufficient to reduce pest pressure and/or crop damage (Tscharntke et al., 2016; Karp et al., 2018). The majority of studies in agriculture have taken a purely taxonomic approach to understanding diversity relationships with ecosystem functions (reviewed by Perovic et al. 2017), and many suggest variable responses of species to habitat manipulation without noticeable changes in function (Loreau & Mazancourt, 2013; Tilman et al., 1997), or species interactions (Ma et al., 2019). This has resulted in an evolved view of the diversity-ecosystem function argument that focuses on the combined function of predators (e.g. pest suppression, prey preference, community stability) rather than the taxonomic identity or effectiveness of individual species (Pillai et al., 2019; McEvoy 2018; Perovic et al., 2017; Díaz et al., 2007; Gagic et al., 2015). The net function of these predator communities is often dependent on how environmental 'filters' such as habitat availability shape community composition and alter interactions between species (Perovic et al., 2017). Therefore, investigating the effectiveness of habitat provisioning for biological control service delivery requires quantifying changes in the functional role of these communities (Gagic et al., 2015; Tylianakis et al., 2010; Maisonhaute et al., 2017).

Trophic interaction networks are often used as a proxy for predator function in agroecosystems (Tylianakis et al., 2010; Poisot et al., 2013; Heleno et al., 2014; Staudacher et al., 2018), but in order to promote functionally beneficial predator communities, it is necessary to understand how predator-prey interactions are shaped by management practices and habitat dynamics of cropping systems (Heleno et al., 2010; Tylianakis et al., 2007). Empirical studies that show how change in habitat complexity influence interactions (Finke & Denno, 2002; Birkhofer et al., 2008; Hughes & Grabowski, 2006) are based primarily on inferences from changes in the abundances of interacting species in the field (i.e. increased predator numbers and reduced pest numbers). Furthermore, direct predator-prey interactions can be challenging to discern due to the complex and cryptic feeding behavior of generalist predators in agroecosystems (Symondson et al., 2002; Kidd and Jervis, 2005; Furlong, 2015). Molecular gut-content analysis (MGCA) has become a widely used method to identify predation on key pests under natural conditions, providing a powerful means for discerning the realized roles of natural enemies and communities in the field (Eitzinger et al., 2018; Harwood et al., 2007; Brown et al., 2015, Szendrei et al., 2010, 2014; Jacobsen et al., 2019; Bouvet et al., 2019; Ingrao et al., 2017; Lundgren and Fergen, 2011, Diehl et al., 2013; Roubinet et al., 2017). MGCA can provide estimates of interactions between entire predator communities, pests, and alternative prey in response to habitat manipulations and seasonal changes in crop growth.

Here we test the hypothesis that early season habitat provisioning and temporal dynamics of crop growth influence the composition of arthropod natural enemies and their interactions with prey in an annual cropping system (Lou et al., 2019; Rosario-Lebron et al., 2018; Rivers et al., 2018; Bowers et al. 2019). We use rye (*Secale cereale* L.) and crimson clover (*Tifolium incarnatum* L.) cover crops grown in a cotton agroecosystem to provide greater early season habitat complexity compared to conventional cotton production. We build on the results of Bowers et al. (2019), and attempt to link enhanced predator diversity to changes in the composition and function of predator communities over time. Predators were collected during each major cotton growth stage (pre-emergence, seedling, vegetative growth, squaring, flowering, boll development) to investigate how these communities and interaction networks change through time, and align with periods of pest activity. Some cotton pests, such as thrips and stink bugs are of high risk at particular time points within the season (thrips on seedling cotton; stink bugs on developing bolls), while other pests (i.e., white flies and tarnished plant bugs) have broad seasonal phenologies. Beneficial predator communities must overlap with these "windows" of pest activity in order to provide effective control. Using MGCA, we investigated how cotton development and the addition of early cover crop residue shape interaction networks of predators, primary pests, incidental cotton pests, and non-pest prey.

We expect cover crop residue to provide both structural habitat (Holland et al., 2016) and fuel for detritus based food webs (Chauvin et al., 2015) in the early season. As residue decays, the growth of cotton creates a uniform late season habitat that is structurally different from early season cotton, regardless of cover crop use. Variation in habitat can alter the availability of alternative prey, and changes to habitat structure due to cover crop use and seasonal cotton growth likely influence the prey communities present. Changes in the abundances of available species can manifest as changes in predator interaction networks (Staniczenko et al., 2017). Thus, habitat differences of cover crop residue and cotton at different development stages may result in a measurable change in community structure and resource use (i.e. consumption of prey). We predict that 1) cotton grown into cover crops will support distinct natural enemy communities compared to conventional management without the use of a cover crop; 2) that predator communities will vary in their consumption of pest and non-pest prey when a cover crop is used, with interaction network characteristics that indicate higher levels of community stability and more generalized feeding habits; and 3) that community composition and trophic interactions will vary across the season (i.e. from early season cover residue to late season cotton).

Methods

Experimental design and study site. We investigated the effects of habitat complexity on predator communities and their function in a Georgia cotton production system by establishing cover crops in the fall of 2016 and 2017 at the UGA Southeast Georgia Research and Education Center at Midville, GA (Burke County, 32°52'15.6"N 82°13'12.0"W). Cover crop plots (0.4 ha) were established in a completely randomized block design and replicated 4 times for a total of 12 plots each year (Bowers et al., 2019). A conventionally managed control (no-cover) was maintained throughout the off-season while crimson clover (27 kg/ha) and rye (67 kg/ha) cover crops were planted early November and chemically terminated and rolled 2 weeks before cotton planting. Cotton was planted into cover crop plots May 5, 2017 and April 28, 2018 using a Unverferth strip till rig, while no-cover plots were disked followed by a rip and bed pass. Plots were irrigated during cover crop growth and the cotton growing season, and were untreated with insecticides throughout the study (for full details see Bowers et al., 2019).

Arthropod collection. Canopy and ground dwelling arthropods sampled using a modified reverse-flow leaf blower and a 1m^2 area quadrat presented as abundance and diversity in Bowers et al., (2019), were used in the current study to analyze the effects of cover crops on trophic structure. In brief, the plots were sampled in three locations randomly selected (at minimum 10 m for any edge) on each six sample dates. All habitat (ground, cover residue, and cotton) within the 1 m^2 quadrat was suctioned (~1 min/sample) until there was no visual arthropod activity detected (Bowers et al., 2019). All samples were placed in plastic Ziploc bags and directly onto ice to be sorted at a later date. Predators were then transferred to vials containing 96% ethanol and preserved at -20^{O} C until identification and molecular analysis.

DNA Extraction. To investigate the effect of habitat complexity on trophic interactions of cotton predators and their prey, molecular gut content analysis (MGCA) was conducted on predators collected during the cotton growing season following recommended best practices (Staudacher et al., 2016, 2018; King et al., 2008). During sorting and identification, all intact, undamaged predators were prepared for molecular gut-content analysis. Predators were cleansed with 10% bleach solution, molecular grade H_2O, and 95% ethanol, dried, and placed in microcentrifuge vials prior to DNA extraction to minimize environmental DNA contamination (Ingrao et al., 2017, Wolf et al., 2018). Clean whole-body predators were pulverized for 30sec in 180 µl PBS using an agitator (Tissue Lyser II; QIAGEN, Chatsworth, CA, USA) and 3 mm grinding balls (OPS Diagnostics), and total DNA was extracted and purified using a QIAGEN DNeasy® Blood and Tissue kit following manufacturer protocols for animal tissue extraction (QIAGEN, Chatsworth, CA, USA), with final elution of 75 µl AE buffer. Each extraction of a 96-well plate included a negative control to test for DNA carry-over during the extraction process. Extracted predator DNA was stored at -20°C for later use in PCR.

Gut-content screening. Extracted predator DNA was screened for the presence of pest and alternative prey DNA using three separate PCR reactions, including two multiplex reactions using the Qiagen Multiplex PCR kit (Qiagen, Hilden, Germany) and a singleplex reaction; all utilizing established primer sets (Appendix B.1). All reactions and primer mixtures were designed following standard procedures for primer and PCR optimization (Staudacher et al., 2016, King et al., 2008; Sint et al., 2014). PCR reactions were designed to test for important economic pests (Lahiri et al., 2018; Athey et al., 2019; Naranjo 2018; Gowda et al., 2016), as well as occasional pests of cotton (Lou et al., 2018; Steckel et al., 2018) and common alternative prey taxa in agroecosystems (Nyffeler and Birkhofer 2017; Appendix B.1). Multi 1 was used to test for the DNA of primary cotton pests: Tarnished plant bugs (*Lygus spp.*) (Hagler and Blackmer, 2013), Southern green stink bug *(Nezara viridula*), whiteflies (*Bemisia tabaci*) (Itou et al., 2013) and Thrips (*Franklinellia spp.*) (Staudacher et al., 2016). A new primer set was designed and optimized for southern green stink bugs following recommended protocols for primer design in Chapman et al. (2013), and Staudacher et al. (2016), see Appendix B.3. All PCR Reactions were run with a Bio-Rad C1000 Touch © Thermal Cycler (Bio-Rad, Hercules, California USA). Multi 1 PCR reactions (12.5 µl) contained 6.25 µl 2x Qiagen multiplex master mix, 1.25 µl 10x primer mix, 0.5 µl 5x Q-solution, 0.3 µl BSA, 2.7 µl PCR grade H_20, and 1.5 µl extracted predator DNA. For mutli 1, PCR protocol was 95°C for 15 min, followed by 34 cycles of 94°C for 30 s, 60°C for 45 s, 72°C for 1 min, and a final extension of 72°C for 5 min. Multi 2 was used to test for the presence of an incidental cotton pest and common extra-guild alternative prey that do not usually have economic significance to cotton production, but may influence interactions with primary pests. Multi 2 tested for aphids (Family: Aphididae) (Staudacher et al., 2016), collembolan (Order: Collembola) (Staudacher et al., 2016), and dipteran (Order: Diptera) (Staudacher et al., 2016) DNA. Multi 2 reactions (12.5 µl) were comprised of 6.25 2x Qiagen multiplex master mix, 1.25 µl 10x primer mix, 1 µl 5x Q-solution, 0.3 µl BSA, 2.2 µl PCR grade H_20, and 1.5 µl extracted predator DNA. Multi 2 PCR protocols were as follows: 95°C for 15 min, and 35 cycles of 94°C for 30 s, 63°C for 1 min 30 s, 72°C for 30 s, and a final extension of 72°C for 10 min. A singleplex PCR reaction was used to screen predators for an additional incidental pest, the two-spotted spider mite (*Tetranychus urticae*) (Krey et al., 2017). Aphids and spider mites are common pests of several cropping systems (Van Emden and Harrington 2017; Agut et al., 2018) but do not consistently reach economically significant levels in cotton in the region (Rosenheim et al., 1997) and are therefore treated here as incidental pests. Screening for spider mites was done with a PCR reaction (12.5 µl) containing 6.25 µl TOPtaq master mix (Qiagen, Hilden, Germany), 0.31 µl BSA, 0.625 µl F primer, 0.625 µl R primer, 3.69 µl PCR grade H_20, and 1 µl of extracted predator DNA. Spider mite reaction was ran using the protocol: 94°C for 3 min, and 44 cycles of 94°C for 30 s, 57°C for 30 s, 72°C for 1 min, with a final extension of 72°C for 1 min. All PCR products were visualized using a QIAxel Advanced System for DNA analysis. Incidents of predation were determined as positive prey DNA

(>0.075 RFUs; Sint et al. 2014). Positive controls for each PCR reaction were included to verify reaction success and band size for multiplex PCR. Predator-prey interactions and trophic network characteristics were compared among cover cropping treatments and time periods.

Data management. Due to inter-annual variation in predator community composition and trophic interactions between treatment and year as well as time period and year, each season was analyzed independently. Predator taxa were pooled at the family level when investigating both community analysis and trophic interactions. Predator groups that were sampled in less than 5 percent of samples across a single season were excluded from community analyses. To investigate the function of treatment specific arthropod communities included in the community composition analysis, only predators included in the community analysis were included in interaction matrices for each treatment or time period. For comparison of interaction network characteristics by treatment, network metrics generated (fun: networklevel; package: bipartite) were pooled by treatment and sample date to ensure large enough networks to generate accurate metrics and still maintain replication of treatments. To investigate the temporal changes in community composition and function in response to changes in habitat, predator communities were pooled by time period (Early, Mid, Late) for each year, with each time period including two major cotton development stages.

Data analysis. The composition of predators and their interactions with cotton pests and alternative prey were analyzed using PERMANVOA models (fun: adonis2; package: vegan) using cover crop treatment and time period (early, mid, late) as fixed effects, and plot as a blocking factor (i.e., strata=plot) to account for repeated sampling of the same plot across each season. PERMANOVA models were based on 999 permutations and Bray-Curtis similarity measures (Legendre & Legendre, 1998). In the case of interactions between cover crop treatment and time, treatment effects at each time point (early, mid, late season) were assessed using separate PERMANOVA models with treatment as a fixed effect for each time point. To investigate the effects of cover crops and time period on commonly used network metrics (e.g. connectance, web asymmetry, links per species, weighted NODF, Shannon diverstiy, H2, niche overlap, functional complementarity; Dunne et al., 2002; Bluthgen et al., 2008; Almeida-Neto et al. 2010; Tylianakis et al., 2007) were compared among treatments and time periods for both sample years using linear models (LM). LMs consisted of cover crop treatment and time period (early, mid, late) as fixed effects. Significant differences in network metrics among treatments and time periods were assessed using pairwise comparisons and adjusted using Tukeys method (fun = lsmeans, package = lsmeans). All statistical analyses were performed in R v 3.3.2 (R Core Team, 2018).

Results

Predator community composition. Overall, 2,675 predators were collected from the field across two sample years. In both years, we found that using cover crops to provide habitat resources significantly influences the composition of predators dependent on the time period within the season (Fig 3.1). In 2017, predator communities were significantly influenced by treatment (PERMANOVA: $F_{2,207}$=13.97, p=0.001), time period (PERMANOVA: $F_{2,207}$=16.16, p=0.001), and an interaction between treatment and time period (PERMANOVA: $F_{4,207}$=6.58, p=0.001). The interaction is explained by significant dissimilarity in predator community composition in early (PERMANOVA: $F_{2,9}$=6.53, p=0.002; Fig 3.1) and mid-season (PERMANOVA: $F_{2,9}$=1.71, p=0.007; Fig 3.1) in 2017. During the late 2017 season, predator community composition was not significantly dissimilar among cover crop treatments

(PERMANOVA: $F_{2,9}=1.95$, p=0.174). Similarly, in 2018, we found that predator community composition was significantly influenced by treatment (PERMANOVA: $F_{2,219}=4.44$, p=0.001), time period (PERMANOVA: $F_{2,219}=29.97$, p=0.001), and an interaction between the two (PERMANOVA: $F_{4,219}=2.89$, p=0.001). This interaction can be explained by the significant dissimilarity of predator communities in the early (PERMANOVA: $F_{2,9}=16.02$, p=0.002; Fig 3.1) and mid (PERMANOVA: $F_{2,9}=4.39$, p=0.005; Fig 3.1) season but lack of differences in late season communities (PERMANOVA: $F_{2,9}=1.28$, p=0.225; Fig 3.1).

In 2017, early season rye and crimson clover communities were dominated by Geocoridae and ground dwelling predators, while conventionally managed plots harbored sparse predator communities containing mostly carabid beetles (Fig 3.2). Ground dwelling spider taxa were common in mid-season rye (Fig 3.2), while conventional plots, and crimson clover appeared to attract more flying canopy predators such as Coccinellidae and *Orius* spp. (Family: Anthocoridae) (Fig 3.2). In 2018, all early season treatments were made up of mostly omnivorous ground dwelling taxa, though in lower numbers in conventional than either cover crop treatments (Fig 3.2). Ground dwelling predators continued to dominate in rye and crimson clover treatments through the mid-season, while conventional plots were shifting to dominance of canopy predators such as *Orius* and lacewings (Fig 3.2). Web building Theridiidae spiders were most common in late season communities across all treatments during the 2018 season, although ground dwelling spiders still made a significant contribution to crimson clover and rye predator communities (Fig 3.2).

Trophic interactions. A total of 2,454 predators were screened for the presence of pest and alternative prey DNA. The interactions between predators and prey in 2017 were significantly dissimilar by treatment (PERMANOVA: $F_{2,445}=7.96$, p=0.001; Fig 3.3) and time period

(PERMANOVA: $F_{2,445}$=15.53, p=0.001; Fig 3.3). In 2018, we found that treatment (PERMANOVA: $F_{2,531}$=14.11, p=0.001), time period (PERMANOVA: $F_{2,531}$=13.30, p=0.001), as well a treatment by time period interaction (PERMANOVA: $F_{2,531}$=3.35, p=0.003) significantly influenced trophic interactions in the field. This is explained by the strong dissimilarity of interactions among treatments in both the early season (PERMANOVA: $F_{2,79}$=6.09, p=0.005; Fig 3.3) and the mid-season (PERMANOVA: $F_{2,119}$=3.09, p=0.009; Fig 3.3) but no difference in interactions in the late cotton growing season (PERMANOVA: $F_{2,175}$=1.59, p=0.172; Fig 3.3). See supplemental for proportion positive of each prey by treatment and time period (Appendix B.4, B.5) and predator taxa (Appendix B.6, B.7).

Network metrics. Both cover crop use and time period within the season significantly influenced several network metrics in both 2017 and 2018 (Appendix B.8, B.9). In 2017, both weighted nestedness (NODF) (Fig 3.4; Appendix B.8) and niche overlap (Fig 3.4; Appendix B.8) were significantly influenced by cover crop treatment, with interaction matrices having increased nestedness in rye compared to no cover and crimson clover treatments (Fig 3.4), and crimson clover treatments having greater niche overlap compared to no cover treatments (Fig 3.4; Appendix B.10). Web asymmetry was influenced by time period (Fig 3.4) and an interaction between treatment and time period explained by the significantly reduced web asymmetry (closer to zero) of no-cover treatments in the early season compared to crimson clover and rye treatments (Appendix B.10). Additionally, links per species, weighted NODF, Shannon link diversity, and functional complementarity were all influenced by time period in 2017, with each increasing as the season progresses (Fig 3.4; Appendix B.10). Specialization (H2), was marginally influenced by time (Appendix B.8), showing reduced specialization later in the season (Fig 3.4; Appendix B.10). In 2018, only functional complementarity was influenced by cover crop treatment (Fig 3.4), with rye treatments having significantly improved complementarity over either both crimson clover and no-cover treatments (Appendix B.9). Links per species and Shannon link diversity were influenced by time period in 2018 (Fig 3.4) with each increasing as the season progresses (Fig 3.4; Appendix B.11) similar to 2017.

Discussion

For ecological intensification to rival current pest management and build sustainability, we must consider timing of ecosystem service delivery, and alignment of effective predator communities with pest infestations. Cover crops used for habitat provisioning bolstered natural enemy communities and increased their consumption of alternative prey, which appeared to help maintain high predator abundance and unique predator community structure in the early season. The use of cover crops improved the function and stability of predator feeding networks over those without additional early season habitat. Our results show that trophic interaction networks can change significantly throughout the growing season, and that the use of cover crops can help maintain stable predator communities in early season cotton. Thus, we demonstrate that cover crops are an effective way to improve the recruitment of early season arthropod communities, and contribute to improving the stability of predator interaction networks in a cotton agroecosystem.

Changes to the structure of predator communities in response to cover crop treatment suggests that in the early season, cover crops improve the abundance and prevalence of ground dwelling predators (Lycosidae and Staphylinidae), while rye is particularly effective at promoting additional spider taxa such as Gnaphosidae and Linyphiidae. Ground dwelling insect predators and spiders respond positively to increasing habitat complexity (Mashavakure et al., 2019; Cotes et al., 2018; Menalled et al., 2018; Rivers et al., 2017) as a result of improved microhabitat and alternative prey availability. Without cover crop residue in field, seedling cotton lacks substantial predator presence, making mitigation of early season pest outbreaks challenging. Therefore, cover crops not only improve the abundance and diversity of taxa present (Bowers et al., 2019), but shift the structure of these communities toward ground dwelling predators which respond favorably to the addition of habitat and food resources. Using MGCA, we identified potential mechanisms for the differential structuring of predator communities and their impact on economically significant prey.

Dissimilarity in predator community structure among treatments reflects differences in resource use in the early and mid-season. Predators in cover crop treatments were supported by high levels of alternative prey, indicated by high frequency of detection of collembola in the diets of predators. Predation of collembola in rye was particularly high and remained a large part of predator diets into the late season. Conversely, predation by the small communities of predators in no-cover treatments were biased toward aphid predation. Without cover crop residue present, predators likely extended their foraging range to the field margins or beyond in order meet their food needs (Rosenheim et al., 1997). This would explain the early contribution of aphids to overall prey consumption in no-cover plots, as aphid are not generally present in high numbers on seedling cotton. Although aphids were consumed in all treatments early season, only in cotton without a cover crop did they make up a substantial proportion of the prey consumed. Thus, cover crops may alter the distribution and activity of predators by providing food resources within the crop area, whereas few predators are maintained in no-cover plots likely due to low prey availability. Sparse predator communities with low diversity may result in interactions skewed by the small number of available predators and a correspondingly simple network structure, with negative implications for the stability and effectiveness of these communities.

We investigated common networks metrics used to estimate the stability and functioning of predator communities (Ma et al., 2019; Bluthgen et al., 2016, 2008; Welti et al., 2017). In general, our analysis indicated more stable predator communities following the use of a cover crop. Nestedness, often interpreted as the asymmetry of interactions between specialist and generalist species (weighted NODF; Almeida-Neto et al., 2011), increased in cotton grown into cover crop residue. Thus, rarely observed species interact with common species more often, increasing the connectedness of rare species to the entire network (Montoya et al. 2006). This may suggest the support of uncommon predator taxa by common collembolan prey in these treatments. Similarly, increased niche overlap in cover crop treatments suggests shared resource use, or redundancy in the predation of prey taxa. Greater overlap in interactions between taxa reduces the likelihood that agricultural management practices (e.g. chemical application, harvest) will reduce community function through the loss of rare species (Memmot et al., 2004; Burgos et al., 2007; Dormann et al., 2009). Additionally, improved functional complementarity in rye cover crop treatments suggests increased consumptive effects of prey by predator assemblages (Frund et al., 2013) compared to crimson clover or no-cover treatments. Although differences in interaction networks are potentially a result of the low number of predators and early interactions in conventional treatments, our results indicate a potential for risk in conventionally managed cotton, with few predators available to control pest outbreaks or recruitment when cotton habitat is sparse (Gomez-Marco et al., 2016, Manandhar et al., 2017; Athey et al., 2016; Harwood et al., 2007).

The trophic effects of cover crop use diminish as the season progresses, yet time proved to be a strong driver of change for the structure and resource use of predator communities. Predator composition shifts from dominance of ground dwelling taxa in the early season to canopy predators (Orius, Theridiidae, Coccinellidae) in the late season. These shifts in composition are likely a result of the early provisioning of resources to ground dwelling taxa, and then the breakdown of these resources and subsequent increase in live cotton vegetation. Furthermore, network metrics indicate that predator communities become more stable as the season progresses. Increasing web asymmetry in the late season results from an increasing number of higher level species with links to available prey. This is to be expected, as predator diversity increases later in the season in response to increasing habitat (cotton canopy biomass) availability (Bowers et al., 2019), while the number prey taxa screened remained consistent. As the number and diversity of links per species increases later in the season, the strength of these individual links may decrease, diminishing the risk of species loss to disturbance and improving network stability; though reducing the opportunity for strong links between predators and primary pests. But, the contribution of aphid prey increased in all treatments as the season progressed, indicating active suppression of this secondary pest regardless of cover crop treatment. The result is aphid populations remaining at non-economically damaging levels due to natural control by natural enemies in the mid to late season.

Predator communities were considerably rearranged in response to cover crop treatments, especially rye, but predation frequency on key pests such as thrips, southern green stink bug, whiteflies, and tarnished plant bug, was not impacted. Indeed, the only primary pest which predators tested positive in any substantial numbers were thrips, although the highest levels of thrips predation were seen in the mid and late season after thrips are of high risk to cotton

(Toews et al., 2010; Mouden et al., 2017). The lack of predation on key pests across all treatments suggests vulnerabilities for the biological control of pests in this system, despite evidence of improved community stability in response to cover crops. Yet, the suppression of incidental pests, such as aphids and spider mites, likely benefit from the more stable and functionally redundant predator communities associated with cover crops.

Our study measured changes in predator community structure and interaction networks in response to different cover crop treatments and cotton growth stage. Although we did not quantify structural differences between cover crops or cotton at different stages, predator community structure and resource use were directly influenced by cover crop treatment as well as time period. We identified increased consumption of alternative prey items as a potential mechanism for predator community responses in the early season, and empirically show network stability changes in response to habitat provisioning and time. Predation of primary pests was low and did not improve in response to predator community change, but without connecting predation rates to prey populations in the field, we are unable to assess how the availability of non-pest prey directly influences prey preference and the control of key pests. Additionally, the predation of pests such as thrips and whiteflies may be underestimated by current molecular methods, as the DNA of small prey can degrade quickly within predator guts, reducing detectability only a short time after consumption (Nguyen et al., 2019; Gomez-Polo et al., 2016). Still, there are likely multiple mechanisms at work to explain reduction in pest pressure in response to habitat management (Bowers et al., 2019), including both predator consumptive effects and bottom-up effects of habitat (Poveda et al., 2008).

Our results suggest predator community stability is greatest in the late season and that early season conventionally managed cotton is vulnerable to thrips outbreaks due to a lack of predatory taxa and simple interaction networks. We show that the use of winter cover crops can reduce the risk of early pest outbreaks by encouraging stable and functional predator communities when there is little cotton habitat available. Future work is needed to assess how altering the availability of prey influences prey preference of predators throughout the season and their control of key pests, by assessing prey population levels and quantifying antagonistic interactions between predators.

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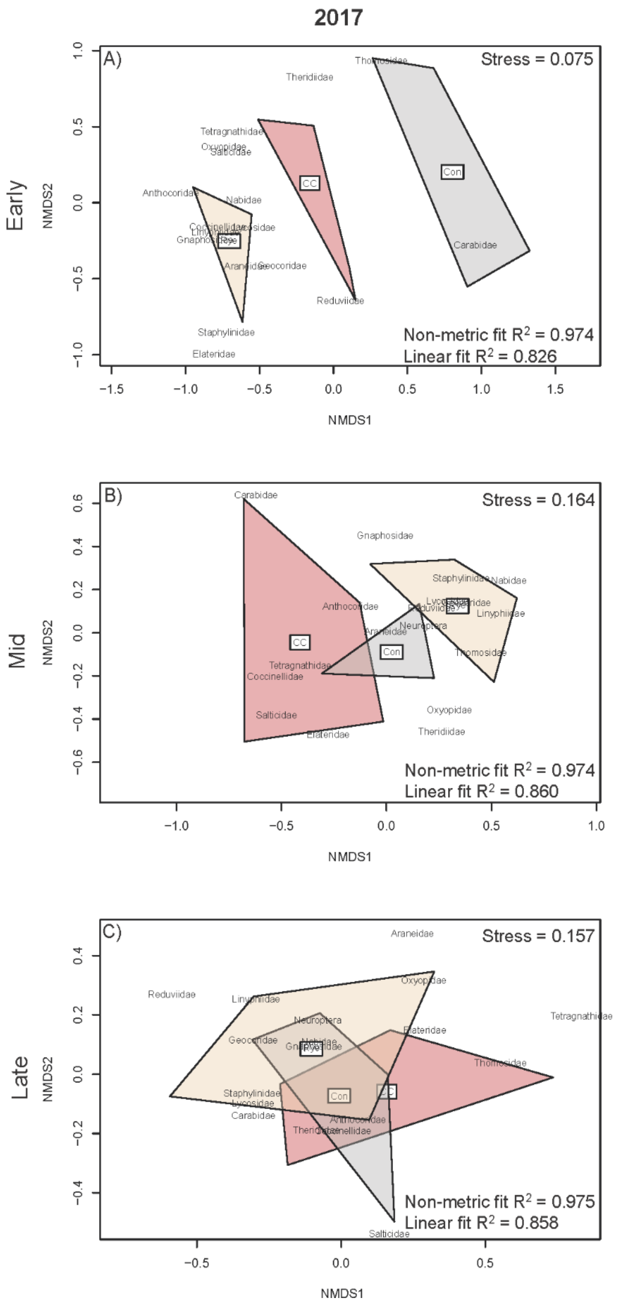

Figure 3.1. Non-metric multidimensional scaling (NMDS) for predator communities sampled from no cover (Con), Crimson clover (CC), and Rye (Rye) treatments in the early (Top), mid (mid), late (bottom) season in 2017 (left) and 2018 (right). Taxa included are present in more than 5% of total samples from each year.

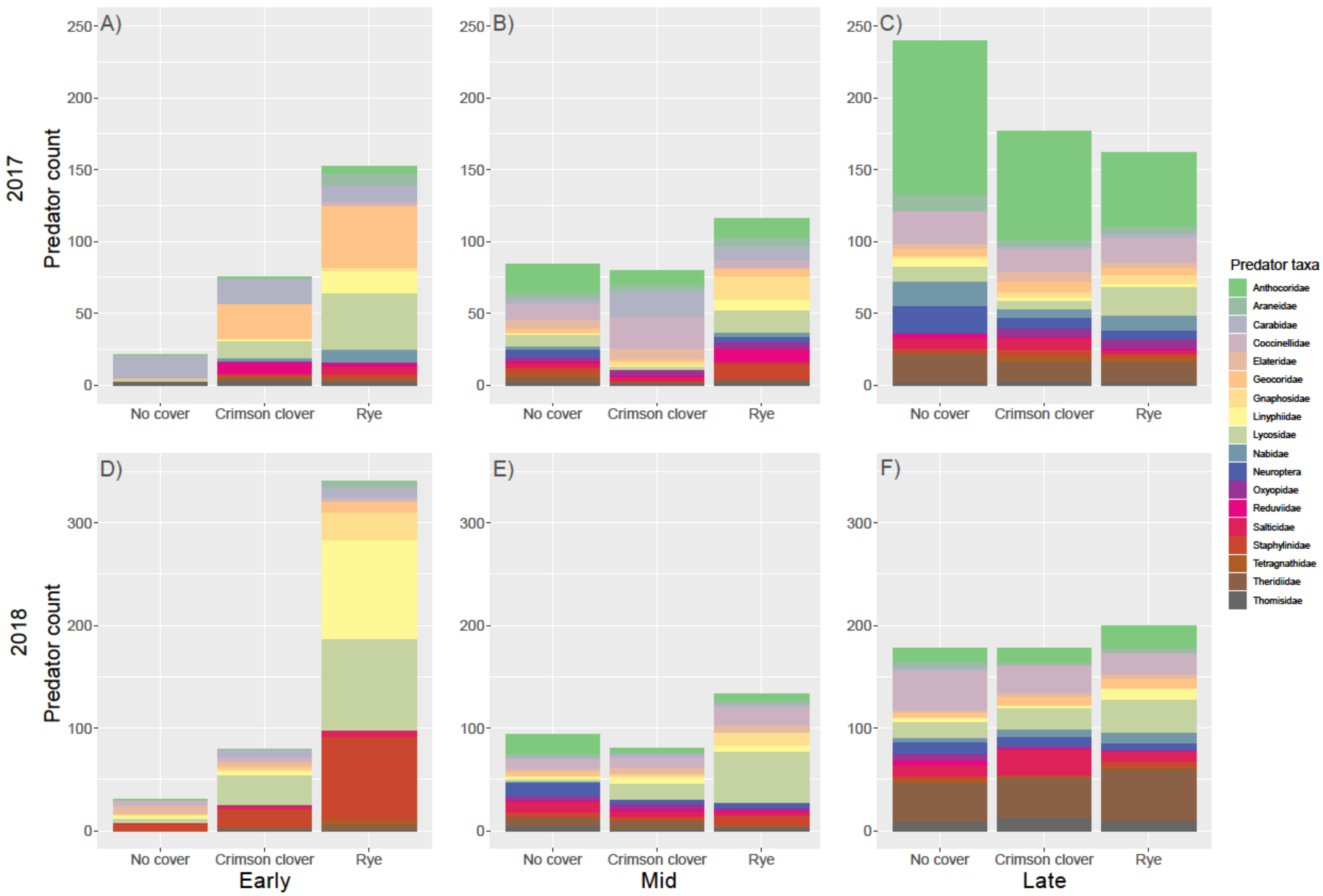

Figure 3.2. Total abundance and composition of predators sampled from each cover crop treatment in the early, middle, and late season for 2017 and 2018. Letters above bars indicate significant dissimilarity (α=0.05) among treatments within the same time period and year.

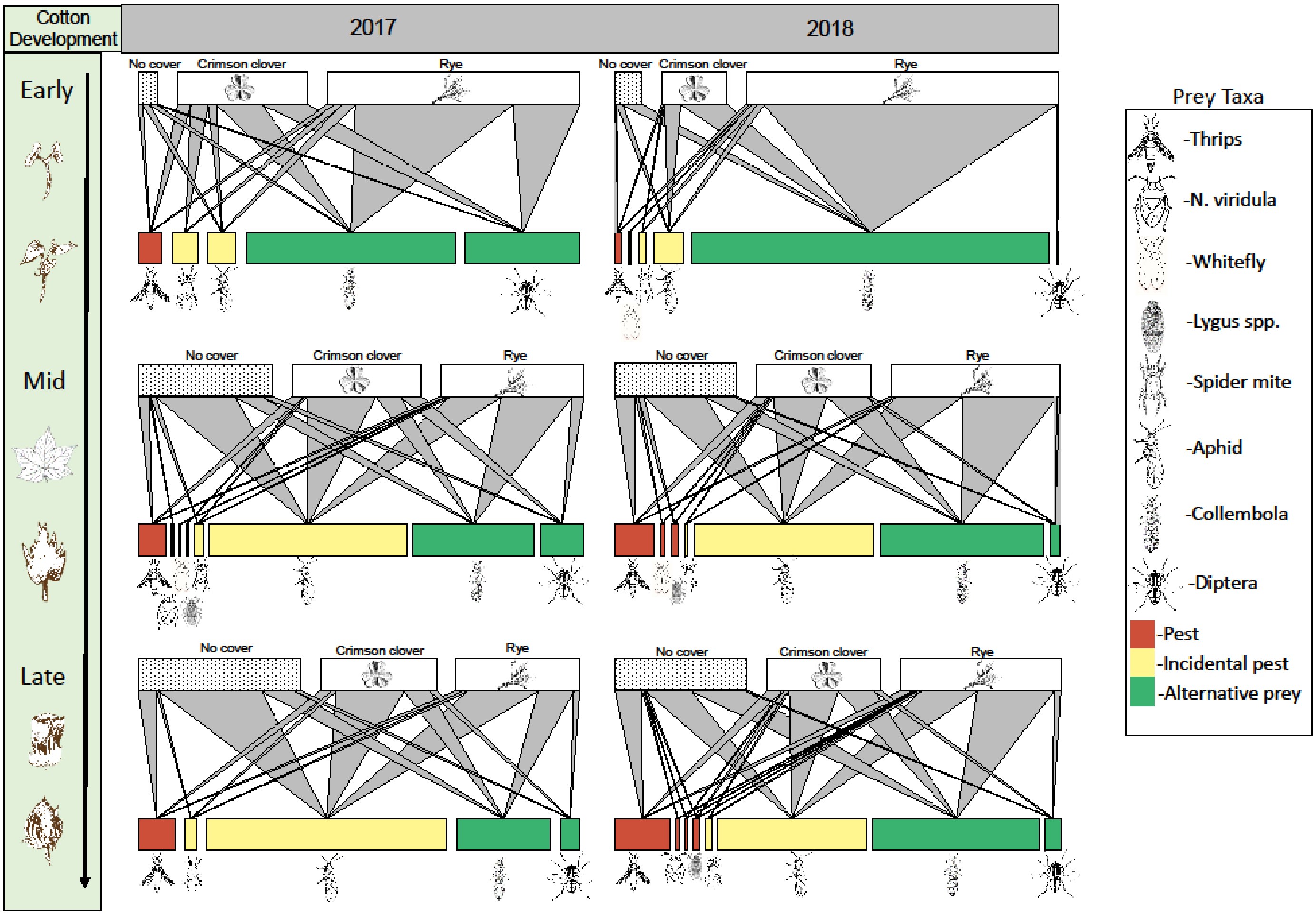

Figure 3.3. Food webs of predators grouped by treatment and their prey items (No cover, Crimson clover, Rye) for early (top) mid (mid) and late (bottom) season in 2017 (left) and 2018 (right). Cover crop treatment is shown on top and prey items on bottom. Predator taxa grouped by cover crop treatments for the upper bars, with the width of the bar indicating predator abundance relative to other treatments. Lower bars indicate prey taxa, with lines linking predators to prey indicating frequency of positive PCR results. Width of bottom bars indicate relative consumption of each prey item across all treatments. Predator or prey taxa with no incidents of predation were excluded.

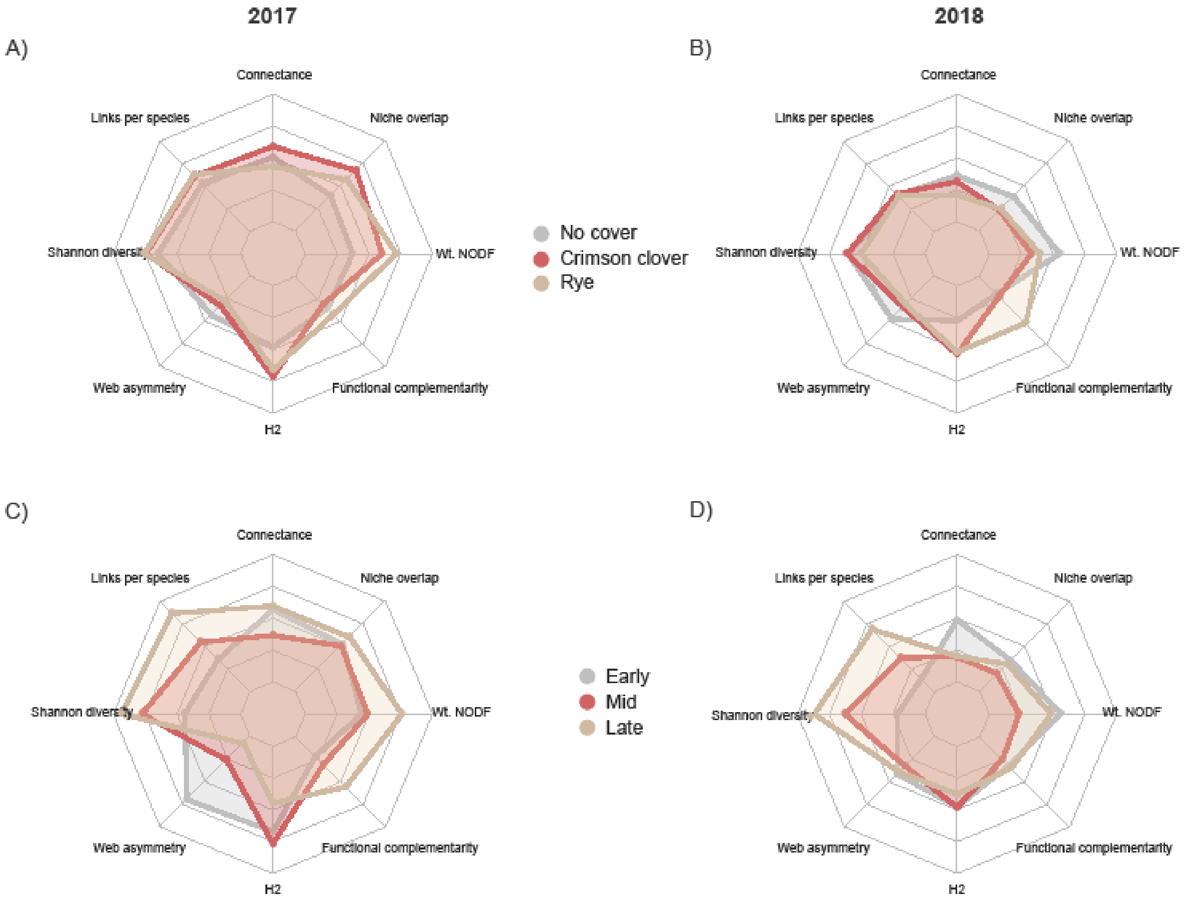

Figure 3.4. Radar plots of selected network metrics including differences in both treatment (top) and time period (bottom) in 2017 (left) and 2018 (right). Metrics include connectance, links per species, Shannon diversity of links, web asymmetry, network specialization (H2), functional complementarity, weighted nestedness (Wt. NODF), and niche overlap. Each metrics is scaled by their individual minimum and maximum values. The inner ring signifies the minimum value and outer the maximum value except for web asymmetry, where the outer ring represents the lowest value (most negative) indicating a higher level of web asymmetry. See supplemental for associated radar plot values and contrasts between treatments.

CHAPTER 4

REFERENCE GUIDE TO COMMON PREDATORS AND PESTS IN GEORGIA COTTON

Introduction

Cotton accounts for nearly 40% of fiber production worldwide and is one of the largest users of insecticides nationally (ERS, USDA 2014). Over 1 million acres of cotton is planted in Georgia each year, and the environmental impacts associated with agriculture can be seen in neighboring and even distant ecosystems. Cotton production and pest management has changed significantly in recent years with the widespread adoption of transgenic cotton varieties targeting herbicide resistance and control of lepidopteran pests. Although pesticide inputs have decreased in cotton, they still account for over 7% of pesticide use in major U.S. Crops, and growers typically spend on average $65 per acre on applications (ERS, USDA 2014). Adoption of transgenic crops has reduced pesticide use, but has also led to increased agricultural intensification through the simplification of farming practices. This increased simplification allows growers to indiscriminately apply insecticides and herbicides targeting non-lepidopteran pests without concern for crop losses, further contributing to the "pesticide treadmill" typically associated with genetic uniformity and reductions in biodiversity (Garcia and Altieri 2005). Cotton pest control in the southern US has shifted focus onto damage caused by early season thrips and a complex of late season heteropteran pests (Naranjo 2010) as well as less consistent pests such as whiteflies and tarnished plant bugs. The response to damage caused by these pests is application of pesticides early in the season for the control of thrips, and later in the season for stink bugs. Augmenting current practices with concrete integrated pest management tactics such as threshold-based pesticide application should promote long-term benefits to ecosystem health including improved soil quality and reduced agrochemical inputs.

Scouting is an important part of crop management and can help to minimize the detrimental effects of pest species by identifying economically significant population levels in field and allowing for timely prescription of treatment. Although application of pesticides including regular calendar sprays have historically counteracted pest problems and improved yields (Matthews 1996), pest management has recently shifted toward practices that reduce pesticide applications and increase reliance on ecologically provisioned services such as biological control (Tilman et al., 2011; Bommarco et al., 2013; Tittonell, 2014; Wittwer et al., 2017). Indeed, research shows that methods to maintain natural enemies and improve movement into crop areas benefits predator communities (Letourneau et al., 2011) and ecosystem service delivery (Landis et al. 2000). Yet, attempts to count predators in field and incorporate them into good scouting practices was abandoned as early as 1960 due to difficulties in incorporating predators into thresholds (Giles et al., 2017; Ramsden et al., 2017) and variability between crop scouting methods (Matthews 1996). Even so, it has been shown that good scouting and education programs can increase the chance that growers will use sustainable IPM practices such as resistant plant varieties and habitat management practices (Ferguson and Yee 1993; Roesch-McNally et al., 2018), increasing yields and reducing risk for those who participated in these programs (Ferguson et al., 1993). The development of more selective pesticide modes of action has further increased the options for ecologically friendly farming practices, allowing for targeting of particular pests with low associated risk to non-target beneficial species such as natural enemies of pests (Torres and Bueno, 2018). To take advantage of these conservation practices, it is increasing necessary to have knowledge on the identity and timing of pests in the field, as well as the presence of natural enemies which may contribute to natural pest control, in order to make informed management decisions and minimize input costs while maximizing production benefits.

Here, my goal was to provide an educational resource to cotton growers, farm managers, and extension agents about natural enemies of cotton pests and the role they play in the field. This includes common natural enemies of cotton pests and how to recognize them, the function of these predators in cotton (i.e. prey they consume), as well as when and where they can commonly be found during the season. Providing information about natural enemies in addition to pests can help growers to recognize the benefit they receive from these commonly found arthropods, and begin integrating their presence and function into management decisions such as if, when and what to spray to mitigate pest pressure with minimal disruption to natural pest control services.

Publication summary

This extension publication covers fourteen predatory taxa from 6 different orders found in cotton agroecosystems, as well as the seven most common pests of cotton in the southeast United States. Information provided for each predator includes common name, diet preferences (from molecular analysis and additional empirical studies), body size, as well as preferred habitat type in the field. Additionally, the timing of predators in cotton fields is shown for the 8 most common types of predators found.

Publication citation and link

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https://secure.caes.uga.edu/extension/publications/files/pdf/C%201161_7.PDF

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WHEN ARE PREDATORS LIKELY TO BE IN MY FIELD?

PREDATOR	MONTH											
	J	F	M	A	M	J	J	A	S	O	N	D
Big-Eyed Bug	⬜	⬜	⬜	🟥	🟥	🟨	🟨	🟨	⬜	⬜	⬜	⬜
Assassin Bug	⬜	⬜	⬜	🟨	🟨	🟥	🟨	🟨	⬜	⬜	⬜	⬜
Damsel Bug	⬜	⬜	⬜	⬜	🟨	🟨	🟨	🟥	🟨	⬜	⬜	⬜
Minute Pirate Bug	⬜	⬜	⬜	⬜	⬜	🟨	🟨	🟥	🟥	🟨	⬜	⬜
Ground Beetle	⬜	⬜	⬜	🟥	🟥	🟥	🟨	🟨	🟨	⬜	⬜	⬜
Lady Beetle	⬜	⬜	⬜	⬜	🟨	🟨	🟥	🟥	🟨	⬜	⬜	⬜
Lacewing	⬜	⬜	⬜	⬜	⬜	🟨	🟨	🟥	🟥	🟨	⬜	⬜
Spiders	⬜	⬜	🟨	🟥	🟥	🟥	🟥	🟥	🟨	🟨	⬜	⬜

🟥 High presence in field
🟨 Medium presence in field
⬜ Low presence in field

Data partially from fields with cover crop residue. All predators can be observed and collected during the day.

Pests

Scouting
for key pests and beneficials is critical for informed and cost effective management decisions.

Thrips
Consistent early-season pest of seedling cotton

Southern green stinkbug
Potentially serious late-season pest of cotton

Whitefly
Potentially serious mid- to late-season pest of cotton

Corn earworm
Pest of cotton bolls

Brown stinkbug
Late-season pest of cotton balls

Tarnished plant bug
Occasional mid- to late-season pest of cotton

Aphid
Potential early- to late-season pest of cotton

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Field Guide to Predators, Parasites and Pathogens Attacking Insect and Mite Pests of Cotton by Allen Knutson and John Ruberson

"Insect Management in Cotton: An Initiative of the Australian Cotton Cooperative Research Centre"

Photos:

Aphids (4387054), Mississippi State University, Bugwood.org

Assassin bug (5367967, 5367980), big-eyed bug nymph (1242039), big-eyed bug (5367925), brown stinkbug (1242026), fire ant close-up (5367982), spined soldier bug nymph (1242093), and tarnished plant bug (5367937), Russ Ottens, University of Georgia, Bugwood.org

Brown lacewing (5351009) and lacewing eggs (5490113), David Cappaert, Bugwood.org

Cobweb weaver (5526012), Sarah Jane Rose, The Ohio State University, Bugwood.org

Corn earworm (1235128), Clemson University - USDA Cooperative Extension Slide Series, Bugwood.org

Damsel bug nymph (5507033) and damsel bug (5507032), Phil Sloderbeck, Kansas State University, Bugwood.org

Fire ant group (2666066) and minute pirate bug (2666062), John Ruberson, Kansas State University, Bugwood.org

Ground beetle (5210002) and lacewing larvae (1475047), Whitney Cranshaw, Colorado State University, Bugwood.org

Lady beetle larvae (1366008), Susan Ellis, Bugwood.org

Lady beetle (5526787), Jim Jasinski, Ohio State University Extension, Bugwood.org

Long-horned grasshopper (1225071), Edward L. Manigault, Clemson University Donated Collection, Bugwood.org

Long-horned grasshopper close-up (2154085), rove beetle (1386032), and wolf spider (5439120), Joseph Berger, Bugwood.org

Lynx spider (1576386), Gerald Holmes, California Polytechnic State University at San Luis Obispo, Bugwood.org

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Spined soldier bug (1472044), Frank French, Georgia Southern University, Bugwood.org

Southern green stink bug (4387037), Phillip Roberts, University of Georgia, Bugwood.org

Tiger beetle (5379921), Jessica Louque, Smithers Viscient, Bugwood.org

Thrips and pupating convergent lady beetle, Schmidt lab

Whiteflies (1599599), John C. French Sr., Retired, Auburn University, University of Georgia, Clemson University, and University of Missouri, Bugwood.org

Drawings:

Spined soldier bug scale drawing by Clercq (2004), with permission from Springer

Cover art and scale drawings for minute pirate bug, ground beetle, and big-eyed bug by Megan McCoy

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Visual Reference Guide to
Common Predators and Pests in Georgia Cotton

Carson Bowers, Jason Schmidt, Melissa Thompson, Phillip Roberts, Michael Toews

UNIVERSITY OF GEORGIA
EXTENSION

Key to Symbols for Predator Habitat Preferences

A — All: found in all or almost all habitat types
C — Canopy: found in the cotton canopy or among cotton flowers
G — Ground: found primarily on the soil or leaf litter
Gm — Grass margins: found in grassy field margins or cover crop residue

Grasshoppers
Tettigoniidae: Orthoptera

Long-horned grasshoppers
Feed on: aphids, thrips, lepidopteran eggs and larvae
1 inch
Gm C

Ants
Hymenoptera

Fire ants
Feed on: lepidopteran larvae and eggs, aphids, soil insects, stink bug eggs, whitefly larvae, spider mites, beetle larvae, most soft-bodied insects, nectar
1 inch
A

Lacewings
Neuroptera

Brown and green lacewings
Larvae feed on: aphids, spider mites, other small insects

Brown lacewing adults are predatory while green lacewing adults feed on pollen and nectar.
1 inch
C

Beetles
Coleoptera

Ground and tiger beetles
Feed on: lepidopteran larvae, aphids, soil insects, weed seeds
1 inch
G

Lady beetles
Feed on: aphids, lepidopteran eggs and larvae, spider mites, cotton nectar, pollen
1 inch
C

Rove beetles
Feed on: aphids, spiders, other small insects
1 inch
A

Spiders
Araneae

Ground hunters
Wolf spider

Canopy web builders
Cobweb weaver

Ambushers/stalkers
Lynx spider

1 inch

Feed on: lepidopteran eggs and larvae, whiteflies, plant bugs and hoppers, aphids, thrips

These spiders are just a few examples of this diverse group of predators found in cotton.

Gm G
C

True Bugs
Hemiptera

Big-eyed bugs
Feed on: lepidopteran eggs and larvae, aphids, mites, whiteflies, plant bugs, cotton nectar, plant sap
1 inch
Gm C

Assassin bugs
Feed on: lepidopteran eggs and larvae, aphids, thrips
1 inch
Gm C

Damsel bugs
Feed on: lepidopteran eggs and larvae, aphids, mites, whiteflies, plant bugs, fleahoppers, beneficials
1 inch
Gm C

Minute pirate bugs
Feed on: lepidopteran eggs and larvae, aphids, mites, whiteflies, thrips, pollen
1 inch
C

Spined soldier bugs
Feed on: caterpillars, beetle larvae
1 inch
C

Figure 4.1. Visual reference guide to cotton predators and pests in Georgia cotton.

CHAPTER 5

SUMMARY AND CONCLUSIONS

There is currently a pressing need to shift from agriculturally intensive management practices such as broad spectrum pesticide applications, high mineral inputs, and increased land use for monoculture production, to more ecologically based management reliant on services underpinned by biological processes such as biological control and natural improvements to soil health. In the present study, we investigated the effects of cover crops for conservation biological control on arthropod communities, their function, and influence on pest pressure as well as cotton production. Results show that cover crops, especially rye, can bolster natural enemy abundance and diversity in the early season. The use of winter cover crops can reduce early thrips pressure on cotton and mitigate the effects of high stink bug pressure while maintaining competitive cotton production compared to more conventional practices.

Few studies have linked habitat management, biodiversity and crop yields. Here we show that cover crops build natural enemy communities early in the season and reduce pest pressure without sacrificing cotton yield or fiber quality. Providing evidence of biodiversity and biological control benefits of cover crops without increases in production cost can help to alleviate grower concerns about the economics of cover cropping strategies and encourage more widespread adoption. Even so, there is often a disconnect between the improvement of natural enemy communities and the provisioning of biological control services, driving the need to investigate mechanisms of pest suppression and how different arthropod communities vary in the delivery of important ecosystem functions (Gonzalez-Chang et al., 2019). Therefore, we investigated how the composition of predator communities and their ecological function (interactions with prey) is shaped by the presence of cover crops throughout cotton development. Cover crops supported distinct predator communities early season, supported by differences in early prey consumption, but late season communities and interactions were similar when cotton habitat is uniform and cover crop residue has diminished. We identified a mechanism by which natural enemies bolster their populations in the early season, namely increased consumption of collembolan prey items in cover crop treatments. This increase in alternative prey availability is likely due to the decay of cover crop residue fueling detritus based food webs, and resulting in the observed increase in predator abundance, diversity, and composition changes seen in rye, and to a lesser extent crimson clover. Although predator recruitment was significantly improved in cover crop treatments, we were unable to link these changes to increased consumption of several important cotton pests, such as stink bugs, whiteflies, thrips, and tarnished plant bugs, indicating a need for improving biological control in this system. Continued work is needed to identify effective predators of pests in this system, and strategies that promote these predators as part of functionally beneficial communities.

Most habitat management studies focus on testing the ‘enemies hypothesis’ suggested by Root (1973) to explain changes in natural enemy effectiveness in response to increasing habitat complexity (reviewed by Gonzalez-Chang et al., 2019; Shields et al., 2018; Rusch et al., 2017; Gurr et al., 2017). We saw a clear reduction in thrips pest pressure on seedling cotton associated with cover crops and an increase in natural enemy abundance and diversity. Yet, we were unable to link reductions in thrips pressure seen to an increase in predation by natural enemies found in cover crop treatments, suggesting that the reduced thrips pressure was not entirely driven by increased consumption of thrips, but some other mechanism. Indeed, Root (1973) also proposed the ‘resource concentration’ hypothesis to explain pest responses to more complex habitats independent of natural enemy effects. This suggests that reductions of pest damage seen in complex environmental may be a result of ‘barriers’ (mechanical or chemical) which make it more difficult for pest species to locate and feed on host plants. Although we found significant changes to the abundance, diversity, and composition of natural enemies in cover crop treatments likely as a result of increased alternative prey availability and consumption, the lack of early thrips predation by these natural enemies suggests changes in the pests’ ability to find and feed on cotton seedlings in these more complex environments. Thrips use both visual and chemical signals to locate hosts (Reitz et al., 2019), and cover crop residue surrounding cotton seedlings early season may hinder thrips recruitment and feeding by masking cotton chemical or visual cues. Additionally, current molecular tools may underestimate predation rates of small prey items such as thrips, which can degrade quickly within predator guts, reducing detectability only a short time after consumption (Nguyen et al., 2019; Gomez-Polo et al., 2016). Regardless of mechanism, cover crops proved effective in reducing thrips pressure even in the absence of foliar applied insecticides, indicating their potential use as a cultural management practice that improves pest management in addition to other aspects of crop protection and system health (e.g., soil health, erosion prevention, weed suppression, mitigation of climate change; Wilson et al., 2019; Panagos et al., 2015; Toler et al., 2019; Kaye and Quemada, 2017; Daryanto et al., 2018).

Alignment of natural enemy productivity with pest infestations is key to effective pest control, yet few studies have investigated how natural enemy function changes across the growing season (but see Staudacher et al., 2018; Roubinet et al., 2018). We investigated how early season cover crop residue, as well as seasonal changes in cotton growth influence the composition of predators, and their interactions with pest and non-pest prey. We found that just after cotton planting, natural enemies communities are distinct in their composition and function in the early season when using a cover crop. The increased consumption of alternative prey in cover treatments promotes abundant and diverse predator communities in the early and mid-season, while sparse predator communities and simple interaction networks are more likely to be found in conventionally managed cotton. Although cover crops harbored communities with improved stability and function indicated by improvements in the nestedness, niche overlap, and functional complementarity of these interaction networks, changes in network level function and stability were more closely tied to seasonal changes than early habitat provisioning. Interaction networks in the middle and late season were characterized by metrics indicating improved stability compared to early season arthropod communities, regardless of treatment. Later season networks had greater nestedness, number of links, and diversity of links, thereby likely reducing the chance predation of a pest species is hindered by the loss of any one predator species. Still, using a rye cover crop early in the season resulted in networks with a greater range of predators than prey taxa (i.e. web asymmetry), increasing the likelihood for more effective suppression of pests when cotton is premature. Thus, providing early season habitat can help with promoting stable natural enemy communities at times crucial to natural pest management. Despite the lack of evidence for the suppression of primary pests, stable predator communities are important for keeping incidental pests such as aphids and spider mites at economically insignificant levels throughout the season.

Despite the challenges in promoting the delivery of ecosystem services and identifying effective communities for biological control function which we have addressed here, some of the most significant barriers to adoption are cultural. The perception of these strategies and barriers in communicating their efficacy to growers and policy makers still significantly hinders widespread adoption of sustainable habitat management strategies into IPM programs (Shields et al., 2018). Because the economic benefits of conservation biological control are not always clear to growers, or easily factored into their production costs, there is a need for continued work focusing of both short and long term economic benefits of cover crops and habitat management strategies that can demonstrate clear advantage to growers that outweighs the cost of adoption. As such, it is important to focus on strategies that promote multiple ecosystem services such as cover crops, to provide the most economic and ecological value for the given inputs. Continued research into crop and region specific service delivery in response to winter cover crops can help with the development of 'recipes' for natural pest control that growers and extension personnel can implement (Gurr et al., 2017; Shields et al., 2018).

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APPENDIX A

CHAPTER 2 SUPPLEMENTAL MATERIALS

Appendix A.1. 2017 full plot management details including planting, irrigation, chemical pesticide and mineral fertilizer applications.

Date	Management
12/2/16	Planted covers
2/14/17	35units N/acre
2/20/17	Spread 1000lbs Lime
3/29/17	1qt Glyphosate (Covers only)
4/17/17	Field Cultivated no-cover plots
4/18/17	30-90-80 Truck Spread
5/3/17	Strip-tilled all plots
5/3/17	1 qt Pendimethalin behind Striptill
5/8/17	Planted Cotton (PHY 490; 7.9 seeds/m)
5/8/17	Applied 10ozs Reflex, 10ozs Diuron, 1 qt Glyphosate
5/8/17	Irrigated .35 in
5/11/17	Irrigated .50 in
5/16/17	Irrigated .35 in
5/18/17	Irrigated .50 in
5/30/17	29ozs Liberty
6/17/17	Irrigated .50 in
6/26/17	0.1ozs Envoke, 1qt Glyphosate, 1qt/100 Surfactant
6/28/17	70 units N sidedressed (all plots)
6/29/17	Irrigated .35 in
7/11/17	1 qt MSMA, 1 qt Diuron, .10 oz Envoke Layby
7/12/17	Irrigated .75 in
7/22/17	Irrigated .75 in
7/25/17	12ozs Mepiquat, .25 lb Boron
7/27/17	Irrigated .75 in
7/28/17	Irrigated .75 in
8/1/17	Irrigated .75 in
8/6/17	Irrigated .75 in
8/15/17	Irrigated .75 in
8/20/17	Irrigated .75 in
8/24/17	Irrigated .75 in
9/1/17	Irrigated .75 in
9/4/17	Irrigated .75 in
10/3/17	4ozs Dropp, 42ozs Ethephon, 10ozs Def
10/31/17	Harvest

Appendix A.2. 2018 full plot management details including planting, irrigation, chemical pesticide and mineral fertilizer applications.

Date	Management
11/20/17	Planted covers
11/27/17	26 units N/acre
11/27/17	Irrigated 1.00 in
1/22/18	Spread 1000lbs Lime
3/5/18	1st cut with disk (No-cover only)
4/2/18	1qt Glyphosate (Covers only)
4/3/18	2nd cut with disk (No-cover only)
4/3/18	30-60-110 Truck Spread
4/20/18	Strip-tilled all plots
4/28/18	1qt Grmoxone, 10ozs Reflex, 10ozs Diuron
4/28/18	Planted Cotton (PHY 440; 3.4 seed/ft)
5/1/18	Irrigated 0.35 in
5/3/18	Irrigated 0.50 in
5/14/18	29 ozs Liberty, 2 pts Warrant
6/9/18	1qt Glyphosate, 2ozs Staple
6/9/18	65 units N side-dressed (all plots)
6/9/18	Irrigated .35 in
6/11/18	Irrigated .35 in
6/23/18	Irrigated .75 in
6/27/18	1 qt MSMA, 1 Qt Diuron, 1 qt COC, .10 Oz Envoke
7/9/18	12ozs Mepiquat, .25lbs Boron
7/9/18	Irrigated .75 in
7/12/18	Irrigated .75 in
7/19/18	Irrigated .75 in
7/24/18	Irrigated .75 in
7/27/18	Irrigated .75 in
8/15/18	Irrigated .75 in
8/19/18	Irrigated .75 in
9/21/18	6ozs Folex, 4ozs Drop, 42ozs Ethephon, 1qt Glyphosate
10/4/18	Harvest

Appendix A.3. Arthropod suction sample dates corresponding to each major cotton development stage.

Cotton stage	**2017**	**2018**
Seed	5/16/17	5/8/18
Seedling	5/31/17	6/1/18
Leafy growth	6/23/17	6/19/18
Squaring	7/19/17	7/10/18
Flowering	8/2/17	7/26/18
Boll Development	8/14/17	9/5/18

Appendix A.4. Total number of stink bugs collected from sweep net samples in each treatment across all sample dates. Counts include both adults and identifiable nymphs.

	2017			*2018*			
Stink Bug Taxa	**No cover**	**Crimson clover**	**Rye**	**No cover**	**Crimson clover**	**Rye**	**Total**
Nezara viridula	13	4	4	11	0	12	44
Euschistus servus	1	0	0	6	5	5	17
Acrosternum hilare	0	0	0	1	1	1	3
Euschistus quadrator	0	0	0	1	0	0	1
Other stink bugs	0	2	1	7	6	3	19
Total	14	6	5	26	12	21	84

Appendix A.5. Total abundance of predators by taxa (family level or higher) in each treatment for 2017 and 2018. Listed in order by most abundant to least (combined 2017&2018).

	2017			*2018*			
Predator Taxa	Con	CC	Rye	Con	CC	Rye	Total
Lycosidae	20	20	74	30	71	180	395
Anthocoridae	126	86	68	32	19	27	358
Coccinellidae	33	38	24	53	55	53	256
Linyphiidae	7	4	26	10	40	137	224
Theridiidae	25	17	19	47	53	62	223
Staphylinidae	6	4	16	14	26	98	164
Geocoridae	9	33	53	12	15	19	141
Carabidae	19	37	25	5	18	16	120
Salticidae	10	13	9	24	34	18	108
Neuroptera	24	7	10	25	24	13	103
Gnaphosidae	2	7	24	1	6	42	82
Araneidae	17	9	19	10	7	15	77
Nabidae	19	8	23	5	7	11	73
Elateridae	10	15	6	12	13	12	68
Thomisidae	6	7	6	14	19	14	66
Oxyopidae	3	11	11	10	8	5	48
Reduviidae	5	9	13	6	5	2	40
Chilopoda	NA	NA	NA	2	12	21	35
Tetragnathidae	4	7	4	4	3	11	33
Dolichopodidae	1	1	1	5	7	9	24
Dermaptera	1	3	5	1	0	7	17
Miturgidae	0	0	0	0	1	4	5
Pisauridae	2	0	0	1	1	0	4
Dictynidae	0	0	1	0	0	2	3
Podisus	0	0	0	0	0	2	2
Mimetidae	0	0	0	1	0	1	2
Anyphaenidae	0	0	0	1	0	0	1
Cubionidae	1	0	0	0	0	0	1
Hahniidae	0	0	0	0	0	1	1
Philodromidae	0	0	0	0	1	0	1
Total	350	336	437	325	445	782	2675

Appendix A.6. Mean (±1SE) predator density (no./m^2) (a) and diversity (H) (b) for each treatment during each major cotton development stage in 2017 and 2018. Results of linear contrasts on the interaction between date and cover crop treatment are indicated with letters where different letters indicate significant differences between treatments at a given cotton stage (α<0.05).

a) Predator Density (no./m^2)

Cotton Stage	No Cover	Crimson Clover	Rye
2017			
Seed	0.81(0.41)^{a}	3.5(0.80)^{ab}	7.0(0.89)^{b}
Seedling	0.75(0.28)	1.92(0.38)	3.92(0.89)
Leafy Growth	2.17(0.35)	2.58(0.47)	6.17(0.86)
Squaring	5.0(0.74)	4.33(0.95)	4.0(0.94)
Flower	8.42(1.05)	5.17(0.83)	7.08(0.91)
Boll Development	11.75(0.85)	9.58(1.69)	7.0(0.98)
2018			
Seed	0.67(0.36)^{a}	3.33(1.42)^{a}	9.67(1.93)^{b}
Seedling	1.92(0.47)^{a}	3.92(0.82)^{a}	21.75(2.55)^{b}
Leafy Growth	2.42(0.61)	2.25(0.60)	5.58(1.10)
Squaring	6.33(0.79)	5.0(0.62)	6.42(0.92)
Flower	9.0(1.34)	8.08(1.19)	9.92(0.94)
Boll Development	6.67(0.87)	6.92(1.78)	8.0(1.18)

b) Predator Diversity (H)

Cotton Stage	No Cover	Crimson Clover	Rye
2017			
Seed	0.0(0.0)^{a}	0.52(0.12)^{ab}	1.15(0.17)^{b}
Seedling	0.11(0.07)	0.31(0.12)	0.65(0.16)
Leafy Growth	0.49(0.13)^{a}	0.40(0.13)^{a}	1.25(0.08)^{b}
Squaring	1.12(0.13)	0.68(0.17)	0.85(0.15)
Flower	1.42(0.11)	1.15(0.19)	1.50(0.14)
Boll Development	1.28(0.10)	1.02(0.13)	1.25(0.12)
2018			
Seed	0.12(0.08)^{a}	0.59(0.16)^{ab}	0.92(0.14)^{b}
Seedling	0.61(0.19)^{a}	0.92(0.15)^{ab}	1.67(0.09)^{b}
Leafy Growth	0.65(0.19)	0.42(0.17)	0.93(0.19)
Squaring	1.45(0.16)	1.39(0.10)	1.36(0.20)
Flower	1.79(0.11)	1.56(0.18)	1.75(0.06)
Boll Development	1.50(0.16)	1.30(0.10)	1.39(0.17)

Appendix A.7. Additional economic value analysis information

The cottonseed yield was estimated using a conversation ratio of 1.412 pounds of seed per pound of lint, which is obtained from the Upland Cotton Loan Calculator Program Decision Aid developed by Cotton Incorporated. Cottonseed prices in each year were obtained from U.S. Department of Agriculture National Agricultural Statistics Service. The prices for cotton lint include the cotton loan price and market price to compare the effect of prices on the profitability of different treatment. Cover crop seed costs come from the actual costs of the field experiment. Cover crops were planted using the costs for no-till drill (Lazarus 2017, 2018). The costs for two additional tandem disk with field cultivator were used for conventional tillage (Lazarus 2017, 2018). Cost for a strip-till rig for cover crop from UGA Cotton Budget (2017, 2018). The costs for row crop planter from Lazarus (2017, 2018) were used for planting cotton. Herbicide costs come from the actual costs of the field experiment and application cost for herbicide comes from Lazarus (2017, 2018), which is the total cost per acre of a self-propelled boom sprayer. Picking and moduling costs come from the Upland Cotton Loan Calculator Program Decision Aid developed by Cotton Incorporated. Ginning costs come from UGA Cotton Budget (2017, 2018). All costs include fuel, lubricants, repairs and maintenance, labor, electricity, depreciation (depreciation is both time-related and use related), and overhead costs (interest, insurance, and housing). Four trips of herbicide were used for conventional tillage, and five trips of herbicide application were used for the cover crop treatments.

Appendix A.8. Mean production values and standard errors (SE) for each cover crop treatment at loan value and market value for cotton crop in 2017 (a) and 2018 (b). Includes price premium based on fiber quality, price at loan and market value for cotton lint, and production cost used for net return ($/acre). The price premium for cotton fiber includes fiber grade and length, cotton micronaire (mic), uniformity, and extraneous matter premiums. Total cost includes the costs of planting cover crop and cotton, herbicide and application costs during the season, and costs associated with picking and moduling costs as well as ginning cost. All units are in USD per acre unless otherwise stated.

(a) 2017

Cover	Value	Price premium (cents/lb)	Lint price (cents/lb)	Lint value	Seed value	Gross return	Total cost	Net return
No cover	Loan	3.81 (0.37)	53.30(0.37)	468.50(20.45)	88.13(3.69)	556.63(24.09)	120.42(0)	394.95(18.71)
Crimson clover	Loan	4.56 (0.15)	54.05(0.15)	485.13(34.26)	90.00(6.43)	575.13(40.68)	170.19(0)	427.38(30.22)
Rye	Loan	4.71 (0.25)	54.20(0.25)	499.63(14.04)	92.38(2.47)	592.00(16.49)	144.39(0)	441.13(12.75)
No cover	Market	4.66(0.56)	80.36(0.56)	706.25(30.46)	88.13(3.69)	794.38(34.09)	120.42(0)	527.33(28.18)
Crimson clover	Market	6.03(0.23)	81.72(0.23)	733.25(51.78)	90.00(6.43)	823.25(58.20)	170.19(0)	505.31(47.74)
Rye	Market	6.11(0.34)	81.81(0.34)	754.25(21.10)	92.38(2.47)	846.63(23.55)	144.39(0)	551.36(19.80)

(b) 2018

Cover	Value	Price premium (cents/lb)	Lint price (cents/lb)	Lint value	Seed value	Gross return	Total cost	Net return
No cover	Loan	1.79(0.82)	53.79(0.82)	447.63(27.42)	89.25(4.64)	536.88(31.98)	127.39(0)	277.36(25.70)
Crimson clover	Loan	3.41(0.58)	55.41(0.58)	510.88(26.92)	99.00(5.15)	609.88(31.97)	171.96(0)	291.79(25.28)
Rye	Loan	3.82(0.29)	55.82(0.29)	423.00(31.04)	81.25(5.96)	504.25(37.00)	149.16(0)	234.47(28.17)
No cover	Market	2.31(1.24)	74.28(1.24)	618.00(37.60)	89.25(4.64)	707.25(42.11)	127.39(0)	447.74(35.90)
Crimson clover	Market	4.76(0.94)	76.73(0.94)	706.88(36.60)	99.00(5.15)	805.88(41.61)	171.96(0)	487.79(35.01)
Rye	Market	5.16 (0.64)	77.14(0.64)	584.63(43.20)	81.25(5.96)	665.88(49.14)	149.16(0)	396.09(40.35)

Appendix A.9. Descriptions of fiber quality metrics tested (USDA, 2004).

Fiber quality metric	**Description**
Lint Yield	Weight of marketable cotton lint (after seed removal). Measured in both lbs/acre and kg/ha.
Color grade	gradations of grayness and yellowness in the cotton based on measurements of both Rd and +B
Staple	Length of cotton fibers in 32nds of an inch
Mic(micronaire)	Cotton's fineness reported to the nearest tenth. Measures resistance to air flow per unit mass
Strength	The fiber strength measurement is made by clamping and breaking a bundle of fibers with a 1/8-inch spacing between the clamp jaws. Results are reported in terms of grams per tex to the nearest tenth. A tex unit is equal to the weight in grams of 1,000 meters of fiber. Therefore, the strength reported is the force in grams required to break a bundle of fibers one tex unit in size.
Rd	Gradation of grayness of cotton fiber measured as % reflectance.
+B	Yellowness of cotton fiber. Greater +B value indicated increasing yellowness.
HVI Length	Length of cotton fibers measured in inches.
Uniformity	Uniformity index is a measure of the degree of uniformity of the fibers in a sample to the nearest tenth. Displayed as a percentage with a higher percentage indicating higher uniformity cotton

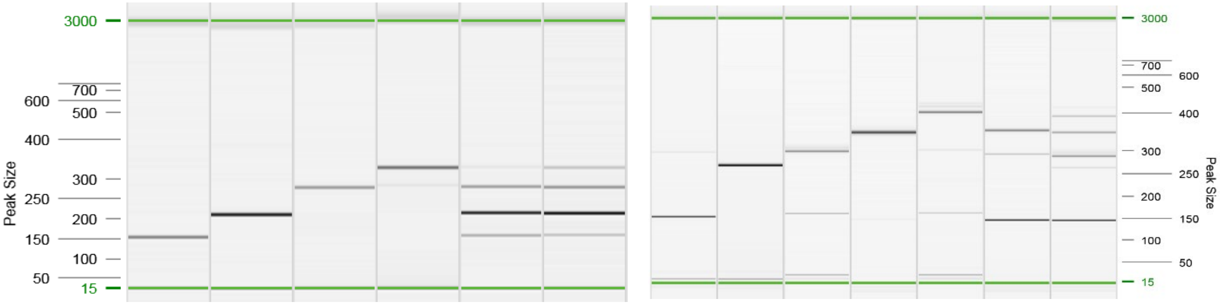
APPENDIX B

CHAPTER 3 SUPPLEMENTAL MATERIALS

Appendix B.1. Additional primer information

Target	**Name**	**Gene**	**5'-3' sequence**	**Amplicon length (in multiplex)**	**PCR assay (conc., uM)**	**Primer source**
Lygus spp.	AY25-lygusF AY25-lygusR	COI	AGGATTTGGACTAATCTCAC ATTACTCCAGTAAGACCTCCT	324	Multi 1 (0.2)	Hagler and Blackmer, 2013
Bemisia tabaci	Bt-F Bt-R	COI	TTGGTGCTCCTGACATAGCTT TAAGCCTCTATGAGTTAATCTTAAA	165	Multi 1 (0.5)	Itou et al., 2013
Frankliniella spp.	S477-thrips A481-thrips	18S	CGGTGTCAAACTGACGCGA GCCCCCGCCTGTCTCC	284	Multi 1 (0.2 F, 0.4 R)	Staudacher et al., 2016
Nezara viridula	SG-223F SG-223R	COI	GCAGAATCTGGAGCAGGAACA CTGTGATCCCAACTGAGCAAAC	219	Multi 1 (0.2)	Supplemental 1
Aphids	S423-aphid1 A424-aphid2	18S	TGGTTCCTTAGATCGTACCCAAG GCCGCGACGGGCC	148	Multi 2 (0.4)	Staudacher et al., 2016
Collembola	S411-springtails1 A415-springtails1	18S	GCTCGTAGTTGGATYTCGGTTT GAATTTCACCTCTAACGTCGCAG	289	Multi 2 (0.1)	Staudacher et al., 2016
Diptera	S414-dipterans1 A416-dipterans2	18S	CCTATCAACTATTGATGGTAGTRTCKWGGA GAAGCACAARWTCAACTWCGAACG	341	Multi 2 (0.5)	Staudacher et al., 2016
Spider mite	Turtic-181-F Turtic-396-R	COI	AGGATTTGGAAATTGATTGA AAAATTATTATTTCAATAGAGGAAGAC	~215	Spider mite (0.6)	Krey et al., 2017

Appendix B.2. Gel images for multiplex PCR results. Shown is results for Multi 1 (left) and Multi 2 (right) including single bands for each prey taxa and positive controls with bands for all prey items screened. Bands shown include whitefly (165 bp), southern green stink bug (219 bp), thrips (284 bp) and lygus (324 bp) for multi 1. Multi 2 results shown include aphid (149 bp), Collembola (289 bp), Diptera (341 bp) as well as additional bands for burrow bug (254 bp) and lacewing (390 bp) although they were not of interest for this study.



Appendix B.3. Molecular gut-content analysis (MGCA) primer design for stink bugs and PCR conditions and modifications for other assays used from the literature.

We optimized a set of COI based primers for screening for *N.viridula* following best practices of creating new multiplex PCRs for diagnostic PCR in gut content analyses (King et al. 2008, 2011, Staudacher et al. 2016). Using PRIMER 3 and PRIMER Blast on NCBI and GenBank sequences: KR037758.1 and KR044112.1, we selected a set of primers that appeared to not amplify other species in the GENBANK database, and provided an amplicon size compatible molecular gut content analysis ~223bp:

SG-223F – 5’- GCAGAATCTGGAGCAGGAACA-3’

SG-223R – 5’- CTGTGATCCCAACTGAGCAAAC-3’

These were then tested in the laboratory for thermocycling conditions and cross-reactivity. The primers did not show cross-reactivity when screened against leg extractions of families we expected in our samples:

1) Araneae families: Araneidae, Corinnidae, Linyphiidae, Lycosidae, Salticidae;
2) Coleoptera families: Carabidae, Coccinellidae; Diptera families: Dolichopodidae, Muscidae;
3) Hemiptera families: Miridae, Anthicoridae, Geocoridae.

The optimal thermocycling conditions were 15 min at 95°C, 35 cycles of 30s at 94°C, 90s at 60°C, 60s at 72°C, and 5 min at 72°C. We followed the same multiplex mix conditions using the Multiplex PCR Master Mix kit (Qiagen), and final primer concentrations were 2mM per primer in the final PCR mix, these were mixed prior to combining with PCR mix and added to form an overall primer concentration in the mix of 10mM as suggested by manufacture (Qiagen).

PCR conditions for other reactions used for Qiagen multiplex kit. For positive controls, we always used a mixed DNA solution containing standardized extraction concentrations of Araneae legs, Carabidae legs, Coccinellidae legs, and the target template. To simulate a mixed template environment for assessing positive results for targets in our cotton molecular trophic interaction diagnostic system. For Lepidoptera (Sint et al. 2014), aphids, Diptera and Thrips (Staudacher et al. 2016) we followed same protocol using same reagents. For spider mites (Krey et al. 2017), we followed same published protocol with Qiagen reagents. For Lygus (Hagler et al. 2013), white flies (Itou et al. 2013) the optimal thermocycling conditions were 15 min at 95°C, 35 cycles of 30s at 94°C, 90s at 60°C, 60s at 72°C, and 5 min at 72°C. In addition, it was possible to multiplex the Lygus, stink bug primers, and white fly primers into a single reaction using the PCR conditions for Qiagen Multiplex Kit: 15 min at 95°C, 35 cycles of 30s at 94°C, 90s at 60°C, 60s at 72°C, and 5 min at 72°C, which formed three clear and consistent bands: 323bp for *Lygus*, 223bp for *N.viridula*, and 139bp for white flies.

Appendix B.4. Predation by treatment and time period in 2017. Proportion of total predators (n) in each treatment that tested positive for each prey item at each time period (early, mid, late) is shown.

trt	time	n	Thrips	Stink bug	whitefly	Lygus	Spider mite	Aphid	Collembola	Diptera
No cover	*Early*	21	0.095	0.000	0.000	0.000	0.000	0.143	0.143	0.048
	Mid	82	0.098	0.012	0.000	0.000	0.049	0.720	0.244	0.098
	Late	213	0.127	0.000	0.000	0.000	0.019	0.714	0.230	0.047
Crimson clover	*Early*	77	0.078	0.000	0.000	0.000	0.104	0.052	0.273	0.273
	Mid	82	0.110	0.000	0.000	0.012	0.012	0.634	0.220	0.195
	Late	148	0.115	0.000	0.000	0.000	0.041	0.682	0.257	0.068
Rye	*Early*	155	0.019	0.000	0.000	0.000	0.026	0.039	0.477	0.206
	Mid	114	0.035	0.000	0.009	0.000	0.018	0.333	0.482	0.079
	Late	141	0.078	0.000	0.000	0.000	0.050	0.738	0.383	0.064

Appendix B.5. Predation by treatment and time period in 2018. Proportion of total predators (n) in each treatment that tested positive for each prey item at each time period (early, mid, late) is shown.

trt	time	n	Thrips	Stink bug	whitefly	Lygus	Spider mite	Aphid	Collembola	Diptera
No cover	*Early*	30	0.033	0.000	0.000	0.000	0.000	0.133	0.433	0.000
	Mid	92	0.163	0.000	0.022	0.043	0.000	0.478	0.228	0.022
	Late	183	0.180	0.011	0.005	0.011	0.000	0.295	0.361	0.016
Crimson clover	*Early*	75	0.013	0.000	0.000	0.000	0.013	0.147	0.413	0.000
	Mid	81	0.123	0.000	0.012	0.012	0.012	0.481	0.358	0.037
	Late	146	0.123	0.000	0.007	0.034	0.014	0.411	0.295	0.055
Rye	*Early*	332	0.006	0.000	0.003	0.000	0.012	0.015	0.596	0.003
	Mid	125	0.024	0.000	0.000	0.000	0.008	0.384	0.552	0.016
	Late	190	0.084	0.011	0.005	0.005	0.026	0.358	0.489	0.042

Appendix B.6. Proportion positive of each prey item by predator taxa (family level) in 2017. Predators can test positive for more than 1 prey taxa, therefore P prey combined does not necessarily total 1. N is the total number of individuals screened from each predator taxa.

Predator taxa	**n**	**Thrips**	**Stink bug**	**whitefly**	**Lygus**	**Spider mite**	**Aphid**	**Collembola**	**Diptera**
Anthocoridae	230	0.104	-	-	-	0.009	0.557	0.083	0.004
Lycosidae	111	-	-	-	-	0.090	0.441	0.874	0.036
Coccinellidae	95	0.084	-	-	-	0.011	0.958	0.242	0.074
Geocoridae	94	0.064	-	-	-	0.106	0.234	0.479	0.457
Carabidae	77	-	-	-	-	0.013	0.117	0.130	0.299
Nabidae	47	0.021	-	-	-	-	0.702	0.149	0.021
Theridiidae	46	0.043	-	-	-	0.065	0.696	0.304	0.022
Araneidae	39	0.128	-	-	-	0.026	0.462	0.333	0.154
Neuroptera	38	0.289	-	-	-	0.105	1.000	0.184	0.026
Linyphiidae	34	0.029	-	-	-	-	0.118	0.588	-
Elateridae	31	0.032	-	-	-	-	0.677	0.129	0.032
Gnaphosidae	30	-	-	0.033	-	-	0.133	0.667	0.033
Salticidae	28	0.393	-	-	-	0.036	0.464	0.429	0.036
Reduviidae	26	0.038	0.038	-	-	-	0.423	0.308	0.269
Staphylinidae	26	0.115	-	-	-	0.038	0.308	0.115	-
Oxyopidae	23	0.043	-	-	0.043	-	0.739	0.087	0.348
Thomisidae	17	0.412	-	-	-	-	0.353	0.412	0.176
Tetragnathidae	14	0.071	-	-	-	-	0.071	0.786	0.214
unidentified	12	-	-	-	-	-	-	0.333	0.083
Dermaptera	9	0.222	-	-	-	0.111	0.889	0.444	0.222
Anthicidae	1	-	-	-	-	1.000	1.000	-	-
Clubionidae	1	1.000	-	-	-	-	1.000	-	-
Corinnidae	1	-	-	-	-	-	1.000	1.000	-
Dictynidae	1	-	-	-	-	-	1.000	1.000	-
Pisauridae	1	-	-	-	-	-	1.000	-	1.000
Tettigoniidae	1	1.000	-	-	-	-	1.000	-	1.000

Appendix B.7. Proportion positive of each prey item by predator taxa (family level) in 2018. Predators can test positive for more than 1 prey taxa, therefore P prey combined does not necessarily total 1. N is the total number of individuals screened from each predator taxa.

	N	**Thrips**	**Stink bug**	**whitefly**	**Lygus**	**Spider mite**	**Aphid**	**Collembola**	**Diptera**
Lycosidae	217	0.009	-	-	0.014	0.023	0.157	0.949	-
Theridiidae	140	0.057	0.014	-	0.007	0.014	0.371	0.521	-
Linyphiidae	123	0.008	-	-	-	0.016	0.065	0.813	-
Staphylinidae	115	-	-	-	-	-	0.035	0.096	0.009
Coccinellidae	113	0.106	-	-	-	-	0.735	0.345	-
Anthocoridae	75	0.133	-	-	-	-	0.347	0.147	-
Salticidae	67	0.328	0.015	0.104	0.090	0.060	0.552	0.478	-
Geocoridae	43	0.116	-	-	-	-	0.093	0.140	0.023
Thomisidae	43	0.372	0.023	-	0.047	-	0.256	0.419	-
Gnaphosidae	41	-	-	-	-	-	-	0.463	-
Elateridae	35	-	-	-	-	-	0.029	0.143	-
Chilopoda	32	-	-	-	-	-	0.031	0.156	-
Hemerobiidae	29	0.241	-	-	-	-	0.862	0.207	0.069
Carabidae	23	-	-	-	-	-	0.130	0.043	-
Araneidae	22	0.091	-	-	-	0.045	0.182	0.318	-
Oxyopidae	22	0.227	-	-	0.045	-	0.500	0.091	0.091
Dolichopodidae	20	0.150	-	-	-	-	0.200	0.100	1.000
Nabidae	20	-	-	-	-	-	0.200	0.050	-
Chrysopidae	20	0.150	-	-	-	-	0.500	0.100	-
Anthicidae	14	-	-	-	-	-	0.071	-	-
Tetragnathidae	12	-	-	-	-	-	0.083	0.750	-
Reduviidae	8	-	-	-	-	-	0.250	-	-
Dermaptera	6	-	-	-	-	-	-	0.167	-
Miturgidae	5	0.200	-	-	-	-	0.600	0.400	0.200
Anyphaenidae	2	-	-	-	-	-	0.500	0.500	-
Mimetidae	2	0.500	-	-	-	-	0.500	-	-
Pisauridae	2	0.500	-	-	-	-	0.500	1.000	-
Dictynidae	1	-	-	-	-	-	-	1.000	-
Philodromidae	1	-	-	-	-	-	1.000	1.000	-
unknown	1	-	-	-	-	-	-	-	-

Appendix B.8. Results of linear models for differences in network metrics for 2017 by treatment and time period. F and P values for each metric are shown for both treatment and time period, with significant differences (α=0.05) shown in bold.

	treatment		Time period		Interaction	
Network Metric	F	P	F	P	F	P
Connectance	0.423	0.6673	1.0842	0.3785	0.2659	0.8926
Web asymmetry	3.6364	0.06958	61.7282	**5.556e-06**	5.7627	**0.01396**
Links per species	0.8636	0.453837	21.9369	**0.0003463**	2.8986	0.08520
Weighted NODF	9.7112	**0.005657**	9.3024	**0.006451**	4.9304	**0.02207**
Shannon diversity	1.2101	0.342416	22.6744	**0.000306**	2.2995	0.13776
H2	2.1097	0.18372	4.0066	0.06229	2.8497	0.09691
Niche overlap	4.3173	**0.04847**	0.5436	0.59857	2.0962	0.16385
Functional complimentarity	0.4836	0.63168	4.5568	**0.04296**	2.1968	0.15027

Appendix B.9. Results of linear models for differences in network metrics for 2018 by treatment and time period. F and P values for each metric are shown for both treatment and time period, with significant differences (α=0.05) shown in bold.

	treatment		Time period		Interaction	
Network Metric	F	P	F	P	F	P
Connectance	0.7758	0.48881	3.5784	0.07186	1.4487	0.29506
Web asymmetry	0.8619	0.4545	0.2535	0.7814	1.8220	0.2088
Links per species	0.0172	0.982933	10.4655	**0.004483**	0.8957	0.50496
Weighted NODF	1.6536	0.24455	3.7604	0.06501	1.6384	0.24698
Shannon diversity	0.3488	0.714643	9.9521	**0.005245**	0.4146	0.79431
H2	3.3273	0.08283	0.5170	0.61302	1.1944	0.37683
Niche overlap	0.9301	0.4294	0.7690	0.4917	1.1626	0.3887
Functional complimentarity	8.2622	**0.009179**	0.6310	0.554037	3.4184	0.05808

Appendix B.10. Mean and SEM values for network metrics of each treatments or time period in 2017. Letters shown results of pairwise comparisons indicating significant differences (α=0.05) between treatments or time periods.

	connectance	web asymmetry	links per species	weighted NODF	Shannon diversity	H2	Niche overlap	Functional complementarity
Con	0.45(0.04)	-0.32(0.10)	1.30(0.24)	18.28(6.43)^{a}	2.40(0.41)	0.18(0.05)	0.27(0.06)^{a}	38.14(14.90)
CC	0.47(0.04)	-0.38(0.06)	1.42(0.14)	29.58(5.16)^{b}	2.65(0.22)	0.27(0.04)	0.46(0.05)^{b}	33.74(8.22)
Rye	0.42(0.03)	-0.41(0.05)	1.44(0.12)	35.02(1.76)^{b}	2.69(0.21)	0.25(0.03)	0.39(0.04)^{ab}	44.42(5.55)

	connectance	web asymmetry	links per species	weighted NODF	Shannon diversity	H2	Niche overlap	Functional complementarity
Early	0.47(0.03)	-0.17(0.06)^{a}	1.04(0.14)^{a}	21.62(7.12)^{a}	1.83(0.26)^{a}	0.25(0.06)	0.36(0.10)	25.39(9.77)^{a}
Mid	0.40(0.04)	-0.42(0.03)^{b}	1.33(0.08)^{a}	24.09(3.94)^{a}	2.74(0.11)^{b}	0.29(0.03)	0.35(0.03)	33.76(6.33)^{ab}
Late	0.48(0.02)	-0.52(0.01)^{c}	1.80(0.07)^{b}	37.17(2.47)^{b}	3.17(0.06)^{b}	0.17(0.02)	0.41(0.03)	57.17(9.37)^{b}

Appendix B.11. Mean and SEM values for network metrics of each treatments or time period in 2018. Letters shown results of pairwise comparisons indicating significant differences (α=0.05) between treatments or time periods.

a)	connectance	web asymmetry	links per species	weighted NODF	Shannon diversity	H2	niche overlap	functional complementarity
Con	0.42(0.07)	-0.26(0.06)	1.21(0.20)	34.22(8.71)	2.42(0.35)	0.20(0.04)	0.37(0.10)	30.22(10.84)^{a}
CC	0.40(0.05)	-0.33(0.04)	1.23(0.12)	20.52(5.30)	2.44(0.31)	0.39(0.07)	0.24(0.05)	33.99(7.39)^{a}
Rye	0.35(0.04)	-0.34(0.04)	1.21(0.11)	24.69(5.80)	2.19(0.35)	0.38(0.06)	0.26(0.05)	77.06(14.85)^{b}

b)	connectance	web asymmetry	links per species	weighted NODF	Shannon diversity	H2	niche overlap	functional complementarity
Early	0.49(0.07)	-0.29(0.07)	0.92(0.04)^{a}	34.86(8.62)	1.55(0.16)^{a}	0.35(0.10)	0.34(0.11)	48.94(23.00)
Mid	0.34(0.04)	-0.34(0.03)	1.18(0.12)^{ab}	14.58(4.88)	2.48(0.31)^{b}	0.35(0.05)	0.22(0.05)	39.15(8.01)
Late	0.34(0.02)	-0.30(0.03)	1.55(0.09)^{b}	30.00(3.79)	3.03(0.08)^{b}	0.28(0.02)	0.31(0.02)	53.17(7.04)