NATURAL ENEMY ABUNDANCE AND BIOLOGICAL CONTROL IN BT MAIZE USING SIMULATIONS OF PREDATOR-PREY INTERACTIONS

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Ecology and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2017

DEDICATION

The spirit of adventure that led to this undertaking and the perseverance to get through the tough times are credited to the inspiration of Ryan Brown.

ACKNOWLEDGMENTS

I give my sincere thanks to my parents who started me on this path and always gave me freedom to pursue my interests however unconventional they may have been; my wife, Jessica, who has been the backbone of our family over the last four years and has inspired me by her own experiences during this time, which have been as profound as my own; my kids, Mason, Avery, and Summer, who have been a great motivation for me to "do my best" but also provided welcome distractions from this effort; my advisor, Dr. Bob Peterson, for his support, insights, and, not least, for putting the "philosophy" into my PhD; my lab mates, Claire Donahoo, Alyssa Piccolomini, Collin Preftakes, and Shavonn Whitten for friendship, support, and great discussions; my committee members, Laura Burkle, David Weaver, Paul Stoy, and Jeff Wolt, for their time, support, and technical advice; Jeff Wolt for giving the initial idea that led to my project; my computer savvy colleagues, Geoffrey Caron-Lormier, Adam Schapaugh, Joao Rossi, Daniel Salinas Duron, and Chris Sehy for sharing their vast technical skills with me; and, lastly, Monsanto company that made it all possible, in particular, Tracey Reynolds and Michael Horak, and other Monsanto colleagues who helped along the way, including Aqeel Ahmad, Dave Carson, Peter Jensen, and Roger Effertz.

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ABSTRACT

The potential effects of genetically modified maize expressing insect-resistant proteins from *Bacillus thuringiensis* (Bt) on natural enemies represent an active area of research highlighting considerable interest in understanding even subtle perturbations in agroecosystems. In the case of Bt maize, indirect effects on natural enemies may occur due to a reduced prey base caused by the desired effect of pest control by the Bt plant. Although these indirect effects may be subtle and difficult to study in the field, a modeling approach offers an alternative, allowing factors related to these subtle effects to be easily explored. In this effort, simulations of interactions between maize, two pests (the European corn borer (ECB) and an aphid), and two natural enemies (a lady beetle and green lacewing) were made using a modified TrophicLink model. TrophicLink is an individual-based model that uses functional ecology and food web network theory to simulate the trophic interactions of individuals and the resulting flow of energy. The individual-based model approach emphasizes the unique experiences of individuals and their trophic interactions leading to system level effects. Pollen utilization, cannibalism, and intraguild predation by natural enemies were simulated to explore the influence of these factors and to test the model. The model performed well in terms of reasonable representation of trophic functional types and interactions between them. The natural enemies were able to reduce a lepidopteran pest population and partially protect yield. The presence of pollen was influential in natural enemy population sizes and the biological control they provide. Cannibalism and intraguild predation caused notable reductions in natural enemy populations, but only small differences in biological control levels. In a second set of simulations involving Bt maize, prey-reduced scenarios included a short-term Bt maize scenario with ECB eggs and young larvae, and a second scenario without any ECB representing regional suppression of ECB by wide adoption of the Bt maize. Lady beetle and green lacewing population mass were similar across scenarios indicating resiliency of the generalist natural enemies to prey removal in the scenarios simulated. These findings are consistent with field study data that have not found consistent effects of Bt maize on natural enemies.

CHAPTER ONE

INTRODUCTION

Based on current trends, the world population will reach more than 9 billion people by 2050, which will require a 70% increase in aggregate global food production (United Nations 2015). To improve agricultural productivity to meet forthcoming demand, existing tools will need to be leveraged and improved and new technologies will need to be developed. Crops produced through biotechnology, commonly referred to as genetically modified (GM) crops, have been identified as a potential tool that can contribute towards increasing crop productivity through resisting insect pest resistance and tolerance to herbicides and environmental stress. Cultivating these crops according to the principles of integrated pest management (IPM) will minimize environmental impacts and delay development of resistance. However, concerns remain that crops derived through biotechnology may be yet another source of potential environmental problems.

GM crops have been approved for cultivation in 28 countries with 19 of these classified as biotech mega-countries growing 50,000 hectares or more (James 2015). Since their introduction in 1996, the adoption of genetically modified crops has been the most rapid of any agricultural technology in history (James 2015) and in some areas they now dominate the agricultural landscape. In the U.S., the percentage of acres planted with genetically modified crops ranges from a low of 76% for insect resistant maize to a high of 93% for herbicide tolerant soybean (USDA 2016). Brazil, the second largest grower of biotech crops behind the U.S. (James 2015), collectively planted 82% of soybean, maize,

and cotton hectares with biotech crops (James 2012). The extensive footprint of biotech crops, which continues to grow, highlights the importance of understanding both the potential negative and positive environmental impacts.

If GM crops are to be a long-term source of improvements in agriculture, it is clear that they cannot be used at the expense of the environment. In fact, the environment may be the most fundamental component for maintaining and improving productivity in the long term. The support system of decision making criteria widely used to manage pests in the agroecosystem, IPM, recognizes the importance of appreciating potential impacts to the environment as a result of pest control actions (Kogan 1998). This is in part due to the recognition of the benefits of a well-managed agricultural environment that provides ecosystem services. One important and perhaps underutilized ecosystem service is the management of pest populations by natural enemies known as biological control. To maximize biological control of pests, existing natural enemy populations need to be actively managed because many agricultural practices are detrimental to natural enemies. Understanding the fit of biotechnology-derived crops within the paradigm of IPM is a key aspect of assessing their potential as an environmentally acceptable tool.

Genetically modified crops have the potential to increase crop productivity by reducing weed competition and pest damage, and allowing plants to better cope with environmental stress. Of particular interest are the GM crops that are resistant to certain pests which have the potential to help conserve natural enemies and enable biological control through the reduced application of broad-spectrum chemical insecticides as a major agricultural practice limiting natural enemy populations. Currently, these insect-

resistant crops control target pests through season-long expression of insecticidal proteins from *Bacillus thuringiensis* (Bt) that exhibit limited toxicity beyond the target pests. Under certain conditions, Bt crops have been documented to reduce broad spectrum chemical insecticide inputs, sometimes dramatically, in Bt cotton and Bt sweet corn (Rose and Dively 2007, Naranjo 2011, Shelton et al. 2013). Reducing insecticide sprays can contribute towards conserving natural enemy populations and enabling biological control of pests (Arpaia et al. 1997, Naranjo and Ellsworth 2009, Lu et al. 2012, Liu et al. 2014, Luo et al. 2014).

Potential negative environmental impacts from Bt crops typically cited include gene flow to wild relatives, reduced biodiversity, negative impacts to non-target organisms, increased prevalence of secondary pests, resistance development, and unforeseen consequences that occasionally occur with new technologies. With the exception of the inevitable development of resistance, experimental evidence as well as the experience growing these crops in the field commercially have to date demonstrated that unexpected negative environmental impacts have not materialized (see discussion below). However, environmental concerns persist over what is still often viewed as a novel technology (Krebs et al. 1999, Peterson et al. 2000, Dale et al. 2002, O'Callaghan et al. 2005, Gatehouse et al. 2011). An additional concern is the accumulation of subtle negative effects on natural enemies from such mechanisms as reduced prey options resulting from the intended removal of target pests by the Bt plant, especially when pests are suppressed area-wide, and prey-mediated effects due to poor quality of intoxicated prey (Hilbeck et al. 1999, Dutton et al. 2002, Schuler et al. 2004, Ferry et al. 2006,

Sanders et al. 2007). Related to the concern of subtle effects caused by Bt crops through prey removal is also the opportunity that Bt crops provide to study natural enemies and how they interact in the agroecosystem. In contrast to broad spectrum insecticide applications, current Bt crops remove certain pests while leaving other pests and natural enemies intact. The removal of part of the prey base available to natural enemies provides a unique experimental situation to study the mechanisms by which a relatively subtle effect on natural enemies might occur. Thus the response of natural enemies to prey reduction, including effects on influential factors such as cannibalism, intraguild predation, and prey preference and prey utilization, can be explored under these conditions.

Though there is strong evidence that suggests Bt crops have not had unexpected effects on natural enemies, it is increasingly important to comprehensively understand any impacts of potential cumulative subtle effects, such as prey removal, as the biotech crop footprint grows. This concern over potential subtle effects on natural enemies, even while significantly reducing broad-spectrum insecticide use, continues to be a testament to the changing perception of the public, agricultural practitioners, and governments about agriculture with regard to the importance of food and environmental safety.

Natural Enemies, Biological Control, and Integrated Pest Management

Before the widespread use of synthetic organic insecticides in the 1940s, crop protection experts used multi-faceted strategies to control pests combining knowledge of pest biology and cultural practices (Kogan 1998). That changed in the post-World War II

era when widespread prophylactic use of organic synthetic insecticides became the single tactic of pest control and research shifted towards the development of new chemistries (Kogan 1998). At that time, heavy use of these insecticides was not a major concern because the practices were highly effective, reliance on one or few options was widely accepted, and any environmental impacts, such as non-target effects on wildlife, depletion of natural enemy populations, secondary pest outbreaks, target pest resurgence, resistance development, and soil erosion, were initially not well appreciated. The negative effects of over-reliance on broad spectrum insecticides, including reduction of natural enemy populations, were being recognized by the late 1950s (Kogan 1998). The importance of having multiple pest control strategies in addition to insecticides became the focus of new pest control programs that eventually gave rise to the integrated pest management paradigm (Kogan 1998). Today IPM is a global practice consisting of decision rules enabling determination of whether a management action is necessary and if so, which action or combination of actions should be used (Kogan 1998). The decision considers economics for the grower as well as environmental and societal repercussions (Kogan 1998).

IPM recognizes the importance of including the environment in the cost-benefit analysis when making pest management decisions in part due to the ecosystem services that can be provided by a well-managed environment. A key ecosystem service valued by IPM is the biological control of pests provided by natural enemies. Current practitioners of IPM generally place a high value on conserving natural enemy populations for this reason. The link between natural enemies and biological control ecosystem services has

been well established (Symondson et al. 2002, Buteler et al. 2008, Naranjo and Ellsworth 2009, Obrycki et al. 2009), but this has not necessarily resulted in across the board conservation of natural enemies in practice. In fact, our increased knowledge of natural enemy biology has highlighted the complexity that arises when trying to apply natural enemy conservation broadly across crops and geographies since the effectiveness of the resulting biological control can vary under different circumstances (Peterson et al. 2009).

Uncertainty in the effectiveness of biological control provided by natural enemies is driven by variability across cropping systems, arthropod communities, geographies, and time. Much of this uncertainty is influenced by abiotic factors, such as weather, life history aspects of natural enemy species, interactions within the natural enemy guild and between natural enemies and their food resources. For example, while increasing natural enemy diversity often increases biological control (Snyder et al. 2006, Bruno and Cardinale 2008), it may also decrease (Finke and Denno 2004, Rosenheim et al. 2004, Finke and Denno 2005), or have no effect on prey suppression (Ives et al. 2005, Bruno and Cardinale 2008). Complicating factors including predation within and across natural enemy species can hinder biological control. Cannibalism within a natural enemy species may suppress natural enemy populations especially since some natural enemies, e.g., lady beetles, often preferentially cannibalize eggs rather than feed on eggs of other natural enemy species (Agarwala and Dixon 1992, Dixon 2000). Cottrell and Yeargan (1998) found that adults and larvae of the lady beetle, *Coleomegilla maculata*, are the main predators of *C. maculata* egg clusters. However, predation of sibling eggs by lady beetles may benefit lady beetle populations when prey is not prevalent (Agarwala 1991, Dixon

2000, Dixon and Kindlmann 2012). Likewise, larval cannibalism in the green lacewing, *Chrysoperla carnea*, was found to be adaptive to sustain populations under low food conditions (Duelli 1981).

Predation across natural enemy species, intraguild predation, has been found to reduce overall biological control in some cases (Cisneros and Rosenheim 1997, Finke and Denno 2004, Rosenheim et al. 2004, Finke and Denno 2005). For example, Cisneros and Rosenheim (1997) investigated a system in cotton including the green lacewing, *C. carnea*; a strong intraguild predator, the assassin bug *Zelus renardii*; and a pest aphid, *Aphis gossypii*. The assassin bug alone was not able to suppress cotton aphid abundance, but the lacewing was able to do so. When present, the assassin bug predated lacewings resulting in an increase in the aphid population. In the absence of a strong intraguild predator, multiple natural enemy species may act in a complementary manner providing additive suppression of pests (Snyder et al. 2006, Bruno and Cardinale 2008).

The highly disturbed nature of annual agricultural systems inherently limits the biodiversity of agricultural fields; however, certain natural enemies are well adapted to such scenarios due to their ability to be highly vagile, polyphagous, effective at searching for prey, highly competitive, and to have high reproductive capacities (Wiedenmann and Smith 1997). Many natural enemies are resilient to uncertainties in unstable and disturbed environments in part by having flexible diets that include non-prey food resources, such as; plant material, fungal spores, extrafloral nectaries, and honeydew deposits (Lundgren et al. 2005b, Lundgren 2009b, Lundgren 2009a, Lundgren et al. 2010, Choate and Lundgren 2013, Schmidt et al. 2013). Utilization of non-prey food resources is another

factor adding complexity to the amount of biological control provided by natural enemies. On one hand, pollen in maize may attract natural enemies to the crop because it is a frequently utilized non-prey food source. However, the increased natural enemy abundance may not translate to additional pest suppression since some natural enemies feed heavily on pollen to the detriment of biological control (Cottrell and Yeargan 1998, Musser and Shelton 2003b).

Ecosystem services provided by natural enemies may be lacking simply because of the inability of the natural enemy to cause a major reduction in the pest population due to a long generation time of the predator relative to the prey (Kindlmann and Dixon 1999). Additionally, we know that the presence of a natural enemy is no guarantee of pest suppression from the many times natural enemies have been introduced to control a certain pest as part of classical biological control, with only a few examples demonstrating complete successes (Hokkanen 1985). Lastly, prey populations may remain unchanged even in the absence of predators because pest mortality inflicted by predators may be replaced by a different source of mortality such as food limitation or abiotic factors (Peterson et al. 2009).

Despite variability in the degree of biological control provided, natural enemies are able to reduce prey populations, to a great degree in some cases. As such, conservation of natural enemy populations continues to be a priority and a fundamental aspect of IPM. Conservation of natural enemy populations has been enabled by having pest control options in addition to broad spectrum insecticides. Some of these options include improved IPM tactics (such as crop rotation) and access to information (e.g.

cooperative extension services and internet resources), herbicide tolerant crops, so called "soft" insecticides with a reduced spectrum of toxicity, and crops with host plant resistance. The advent of herbicide-tolerant crops has allowed for reduced or no tillage practices which benefits soil-dwelling natural enemies. Insecticides with a narrow range of activity against insects enable biological control through conservation of natural enemies. Among insect resistant crops are those that were obtained via breeding to have antixenotic or antibiotic effects on pests and, more recently, those produced using biotechnology to insert genes that confer resistance to the feeding of only certain targeted pests. Like narrow-spectrum insecticides, these tools can reduce applications of broad-spectrum chemical insecticides and encourage biological control.

Potential negative implications remain for natural enemy populations even with these tools. Some tools continue to be lost due to evolution of resistance, which can result in a return to broad-spectrum insecticides. For example, resistance development has been documented for Colorado potato beetle, *Leptinotarsa tridecemlineata*, against imidacloprid (Alyokhin et al. 2007), and western corn rootworm, *Diabrotica virgifera virgifera*, has developed resistance to the Cry3Bb1 and mCry3A proteins expressed in certain Bt maize products (Gassmann et al. 2014). Also, the previously effective method of crop rotation was lost for the northern corn rootworm, *D. barberi*, when the larval stage of the beetle developed extended diapause (Ostlie 1987) and for *D. v. virgifera* when a portion of the population began ovipositing in soybean fields in a limited geography (Gray et al. 1996, Barna et al. 1998). Some of our current tools continue to affect natural enemy communities that we are trying to conserve in more subtle ways than

those associated with broad spectrum insecticides. Herbicide tolerant crops allow for efficient control of weeds, which has been cited as a threat to biodiversity (Heard et al. 2003) which could have implications for the biodiversity of natural enemies. Soft insecticides may have overall more favorable safety profiles (e.g., low mammalian toxicity, reduced activity spectra, low persistence in the environment); however, some have relatively broad spectra of activity which has implications for natural enemies. An example is the controversy that has engulfed the commonly used neonicotinoid seed treatments with respect to effects on honey bees (Gross 2013). As discussed previously, Bt crops have the potential to negatively affect natural enemies in an indirect way through prey removal.

We have come a long way in our knowledge of natural enemies and the biological control they can provide. However, we are limited in our understanding of the degree of biological control provided by natural enemies across the many cropping systems, geographies, and temporal scales. This is in part because studying these factors in isolation in the field is difficult and prohibitively expensive and time consuming. A key objective in this area is to increase certainty around the ability of natural enemies to provide biological control across the diversity of scenarios. This will further solidify natural enemy conservation as a tool for IPM. Bt crops, which have a good potential fit as an IPM tool (Duan et al. 2003, Romeis et al. 2008, Lundgren et al. 2009, Naranjo and Ellsworth 2010), provide a unique scenario to further build our knowledge of the effects of conserving natural enemy populations since current products control only certain pests while leaving the remaining pests and natural enemies intact.

Current Understanding of Potential Effects of Bt Crops on Arthropod Communities

Bt Proteins

Early research on the insecticidal proteins of Bt found that they have a relatively narrow spectrum of activity. With the increased adoption of Bt crops, numerous specific studies have confirmed and in some cases refined the narrow range of activity that these proteins have, some of which are referenced below. The narrow range of activity is based on factors such as gut pH, activation by gut proteases, binding of receptors in the brush border membrane of midgut epithelial cells, membrane insertion, followed by pore formation and cell leakage (Schnepf et al. 1998). Examples of the specificity of Bt proteins include the Cry1 family of proteins that are restricted within the Lepidoptera and the Cry3Bb1 protein which exhibits activity restricted to the family level within the Chrysomelidae.

Exposure of Natural Enemies to Bt Proteins

A number of potential routes of exposure to Bt proteins have been identified for predators and parasitoids. Many predators are facultative feeders of plant materials including leaf tissue, pollen, plant sap, extra-floral nectarines, that may directly expose them to the proteins (Wackers 2005, Lundgren 2009b). Consumption of pollen is especially relevant in maize because copious amounts are produced during a concentrated period of time and the pollen is widely used by insects as a food resource. Lundgren (2009b) has compiled information on the wide consumption of pollen by lacewing adults and likely larvae, heteropteran predators like *Orius* spp., *Geocoris punctipes,* and *Nabis*

spp.; Carabidae, syrphid adults, predatory mites, lady beetle larvae and adults, and honey bees. Incidental consumption of pollen, and thus exposure to Bt proteins, also occurs through pollen covered prey, mycophagy (Lundgren 2009b), web consumption of web building spiders (Ludy and Lang 2006b). Many natural enemies also feed on honeydew excreted by aphids; however, Bt proteins are largely absent from phloem tissue (Head et al. 2001, Raps et al. 2001, Romeis and Meissle 2011).

Soil dwelling organisms, particularly decomposers, may also be exposed to Bt proteins via root exudation or tissue degradation; however, the proteins have been found to degrade relatively quickly and do not accumulate from year to year (Head et al. 2002, Dubelman et al. 2005, Sanvido et al. 2007, Icoz and Stotzky 2008). Natural enemies may also be exposed to Bt proteins through their prey or hosts through tri-trophic interactions. Studies have detected and quantified the amount of Bt proteins in a variety of herbivores and assessed for potential effects on predators and herbivores (see below).

Lab and Greenhouse Studies

An environmental risk assessment (ERA) is required for biotech crops before commercialization of the product. An assessment of potential impacts of arthropods is a major focus of the ERA especially for those biotech crops that are insect resistant. The core data for assessing potential non-target arthropod effects of biotechnology-derived crops are produced according to a tiered framework (Garcia-Alonso et al. 2006, Romeis et al. 2006) where, in the earliest tier, a battery of key arthropods with both agricultural and worldwide relevance are tested at doses well above those typically expressed in the

plant. If the results of the first-tier studies require refinement then subsequent tiers are used to clarify previous results under progressively more realistic situations, ultimately under field conditions if needed. In the case of Bt crops expressing Bt proteins, the tiered testing seldom progresses beyond the first-tier laboratory tests due to the relatively narrow activity spectrum of Bt proteins. The companies that have produced the products have conducted laboratory studies to characterize the spectrum of activity and confirm the narrow range of activity (Duan et al. 2002, Duan et al. 2006, OECD 2007, Duan et al. 2008b). Numerous additional studies have been conducted in addition to those sponsored by the companies and these have further confirmed the narrow spectrum of activity of Bt proteins (Lundgren and Wiedenmann 2002, Meissle et al. 2005, Li et al. 2008, Meissle et al. 2011, Lumbierres et al. 2012, Wang et al. 2012, Tian et al. 2013, Li et al. 2014).

Many other lab, greenhouse, and field study evaluations have been conducted to assess for potential tri-trophic effects as a result of natural enemies feeding on prey that have ingested Bt proteins after feeding on crop plant tissue (Harwood et al. 2005, Lundgren and Wiedenmann 2005, Meissle et al. 2005, Obrist et al. 2005, Bai et al. 2006, Harwood and Obrycki 2006, Harwood et al. 2006, Obrist et al. 2006, Torres et al. 2006, Kim et al. 2008a, Kim et al. 2008b, Torres and Ruberson 2008, Alvarez-Alfageme et al. 2009, Li et al. 2010, Li and Romeis 2010, Tian et al. 2010, Alvarez-Alfageme et al. 2011, Romeis and Meissle 2011, Digilio et al. 2012, Tian et al. 2012a, Tian et al. 2012b, Tian et al. 2013, Tian et al. 2014a, Tian et al. 2014b, Wu et al. 2014). Tri-trophic studies have demonstrated that Bt protein levels do not accumulate across trophic levels and that

predator and parasitoids have not been unexpectedly affected by trophic transfer of Bt proteins to date.

Field Biodiversity and Arthropod Abundance Field Studies

Numerous field studies investigating Bt crops and overall arthropod diversity and non-target arthropod abundance have been conducted across geographies. Local field evaluations are commonly required for cultivation approvals of Bt crops in each country and the intense interest surrounding biotech crops has encouraged many additional trials. As expected, some field studies have found reductions in parasitoid wasps that specialize on the target pest. For example, in a field study testing Bt maize, Pilcher et al. (2005) documented a decline in abundance of the braconid parasitoid wasp, *Macrocentrus cingulum*, presumably due to the removal of the lepidopteran host larva, *O. nubilalis*. Overall, field studies have not found negative effects on non-target arthropods including natural enemies in the main Bt crops including lepidopteran-resistant cotton (Li et al. 2002, Liu et al. 2002, Wan et al. 2002, Wu and Guo 2003, Sisterson et al. 2004, Hagerty et al. 2005, Head et al. 2005, Naranjo 2005a, b, Whitehouse et al. 2005, Torres and Ruberson 2006, 2007, Whitehouse et al. 2007, Naranjo and Ellsworth 2009, Li et al. 2012, Lu et al. 2012, Xu et al. 2012, Li and Liu 2013, Liu et al. 2014, Whitehouse et al. 2014, Yang et al. 2014) and lepidopteran, coleopteran, or both lepidopteran and coleopteran resistant maize (Orr and Landis 1997, Pilcher et al. 1997, Lozzia 1999, Wold et al. 2001, Bourguet et al. 2002, Al-Deeb and Wilde 2003, Al-Deeb et al. 2003, Dively et al. 2003, Volkmar and Freier 2003, Candolfi et al. 2004, Devare et al. 2004, Manachini

and Lozzia 2004, Ahmad et al. 2005, Bhatti et al. 2005a, Bhatti et al. 2005b, Bitzer et al. 2005, Daly and Buntin 2005, de la Poza et al. 2005, Dively 2005, Mullin et al. 2005, Pilcher et al. 2005, Ahmad et al. 2006, Ludy and Lang 2006a, Rose and Dively 2007, Toschki et al. 2007, Farinos et al. 2008, Rauschen et al. 2008, Rauschen et al. 2009, Rauschen et al. 2010b, Peterson et al. 2011, Alcantara 2012) . Some studies have reported that the reduced chemical insecticide inputs have allowed natural enemies to suppress pest populations, which has enabled the biological control services of natural enemies to delay evolution of pest resistance to the Bt proteins (Arpaia et al. 1997, Heimpel et al. 2005, Gassmann et al. 2008, Gassmann et al. 2012, Onstad et al. 2013, Liu et al. 2014).

These typically short-term field studies have not detected consistent or measurable effects in natural enemy populations even as the target pest(s) have been removed from these systems. In contrast to a lack of effects against natural enemies in Bt crop field trials, common agricultural practices result in clear impacts even at the relatively small plot scale, including tillage (Brust et al. 1985, Hammond and Stinner 1987, House and Alzugaray 1989, Lietti et al. 2008, Pineda et al. 2012), crop variety (Isenhour et al. 1989, Chacon et al. 2012), crop type (Hammond and Stinner 1987, Pfannenstiel and Yeargan 1998), field-edge structure (Varchola and Dunn 1999, Holland et al. 2003, Holland et al. 2016), and insecticide application (Newsom 1967, Brust and King 1994, Knutson et al. 2011).

Off-field Non-target Effects

Losey et al. (1999) demonstrated that the Bt protein, Cry1Ab, could cause mortality of monarch butterfly larvae if enough Bt maize pollen was applied to a milkweed leaf. Subsequent studies assessing actual exposure of monarch butterfly larvae under realistic field conditions determined that mortality due to Bt maize pollen was exceedingly low (Pleasants et al. 2001, Sears et al. 2001). In addition to highlighting the importance of actual exposure to Bt proteins as well as hazard (i.e., toxicity), the monarch butterfly experience brought to the forefront the importance of addressing potential effects of, and risks to, off-field non-target butterflies and other arthropods especially those with threatened or endangered status. This sparked a number of studies examining other species of butterflies, including endangered species, all of which found that negative effects due to Bt maize were unlikely (Wraight et al. 2000, Wolt et al. 2005, Peterson et al. 2006, Perry et al. 2010). However, questions remain on this topic, at least in theory, which reflects the continued concern by the public (Lang and Otto 2010, Holst et al. 2013).

Meta-analyses

In an effort to strengthen our overall knowledge of the potential impact of Bt crops on natural enemies and other non-target arthropods, compilation reviews have been conducted as well as collective meta-analyses of existing data on Bt crops and natural enemies. In a review of lab, greenhouse, semi-field, and field studies, Romeis et al. (2006) found no direct effects of Bt proteins on natural enemies fed genetically-modified

crop plant tissue or non-susceptible (i.e., healthy) prey for confined studies. In the field setting, the abundance of natural enemies, other than specialist parasitoids, and biological control were generally similar or somewhat lower between Bt crop plots and untreated control plots; however, abundance in insecticide treatments was often notably lower than Bt crops (Romeis et al. 2006). The findings from Romeis et al. (2006) are consistent with other results from meta-analyses that focused on field data from non-target organisms and Bt crops (Marvier et al. 2007, Wolfenbarger et al. 2008, Comas et al. 2014). A meta-analysis of 25 honey bee studies concluded that Bt proteins had no effect on honey bee survival (Duan et al. 2008a). The assumption that lab studies used in the tiered approach to ecological risk assessment are representative of potential impacts at the field level was confirmed in a meta-analysis of lab and field data (Duan et al. 2010). The conclusion of this study was that the lab studies, including both direct exposure assays and tritrophic assessments, were consistent with or more conservative than field data (Duan et al. 2010). Other overall reviews of Bt crops (O'Callaghan et al. 2005, Sanvido et al. 2007). Another study that focused on the coleopteran resistant maize that expresses the Bt protein Cry3Bb1 reported no adverse effects of IR crops based on the information at hand. In an overall review of genetically-modified insect-resistant crops, Gatehouse et al. (2011) conclude that while some minor impacts have been recorded from the many studies conducted on these crops it is important to position those finding against the much more clear effects resulting from chemical insecticides. Lastly, in an overall review of the safety of biotechnology-derived crops over the last ten years, Nicolia et al. (2014) evaluated “original research papers, reviews, relevant opinions, and reports” of all of the

major issues that were debated and concluded that no significant risks exist with the use of biotechnology-derived crops.

In contrast to the above meta-analyses and reviews, reviewed the Bt crop natural enemy laboratory data using a modified meta-analysis and found that natural enemies were directly negatively affected 21% of the time versus a 5% positive effect. A rebuttal to Lovei et al. (2009) asserted that the conclusions made are problematic because the analysis method was flawed, host-prey mediated effects were treated as direct effects, the apparent effects were not placed into an ecological context, and conclusions were collectively made for both narrow spectrum Bt proteins and more broad spectrum lectins and proteinase inhibitors (Shelton et al. 2009).

Collectively, the studies on Bt crops have not found unexpected effects and have generally found that Bt crops can be compatible with natural enemies and IPM programs. The numerous studies have confirmed expected results such as the narrow spectrum of activity of Bt proteins, lack of accumulation of Bt proteins as they pass through higher trophic levels, and the only consistently detected effects for natural enemies are for those specialist parasitoids that require the target pest as a host. Though the uncertainty of effects on non-target arthropods is often mentioned in the literature, there are only a few references that are cited in support of this uncertainty and these references identified either hazard without consideration for exposure or prey quality-mediated effects on natural enemies as opposed to direct toxicity of the Bt proteins (Hilbeck et al. 1998, Losey et al. 1999, Groot and Dicke 2002, Lovei and Arpaia 2005, Lovei et al. 2009).

More specifically, these studies identified secondary or indirect effects of Bt crops discussed above or hypothesized impacts that have not been observed.

Long Term, Landscape Effects

As detailed above, a wealth of information has been generated on the activity spectrum of the Bt proteins expressed by these crops, routes of exposure, lack of accumulation of Bt proteins in the soil or across trophic levels, lack of tri-trophic effects, and off-field non-target effects. This information is supportive of the relative safety of Bt crops when extrapolated to the long term and landscape level; however, concerns over potential long term and landscape effects of Bt crops persist. Long term and landscape effects that have been anticipated include pest resistance to Bt proteins, area-wide pest suppression, secondary pest emergence, reduced insecticide applications, impacts on off-field non-target organisms including threatened and endangered species, and changes in in-field natural enemy populations. Evolution of pest resistance to Bt proteins, area-wide pest suppression, secondary pest emergence, and a reduction of insecticide use have already been documented and each has implications for natural enemies. The only species to develop field-evolved resistance to the long used Bt spray formulations is diamondback moth, *Plutella xylostella*, which first occurred in the Philippines (Kirsch and Schmutterer 1988) before occurring in other areas as well (Ferre and Van Rie 2002). Resistance to Bt proteins expressed by Bt maize has occurred in *Busseola fusca* resistant to Cry1Ab in South Africa; fall armyworm, *Spodoptera frugiperda*, resistant to Cry1F in Puerto Rico; *D. v. virgifera*, resistant to Cry3Bb1 in the U.S., and the pink bollworm,

Pectinophora gossypiella, resistant to Cry1Ac in India (Dhurua and Gujar 2011). The key concern relative to natural enemies and the pests evolving resistance to Bt proteins is that the loss of Bt proteins as an option for pest control results in the return to broad spectrum insecticides.

Area-wide pest suppression has been predicted for pest species that have a narrow host range, are highly susceptible to the Bt protein, and are in environments where these crops dominate the landscape (Freeman and Smith 1997). Area-wide suppression has been documented for the European corn borer, *Ostrinia nubilalis*, in the Corn Belt of the U.S., for *P. gossypiella* in the southwestern U.S. (Carriere et al. 2003), and *Helicoverpa armigera* in China (Wu et al. 2008) and for *O. nubilalis* in the U.S. Corn Belt (Hutchison et al. 2010). Area-wide suppression of target pests results in permanent removal of a potential food resource for natural enemies and could also result in area-wide removal of specialist parasitoids.

Because these crops have reduced insecticide applications in some cases and the Bt proteins have a relatively narrow spectrum of activity, secondary pests incidentally controlled by insecticide sprays applied for key pests have become more prominent. Cotton may provide the most striking example of this occurrence as true bugs have elevated to key pest status in Australia, China, South Africa, and the U.S. (Wu et al. 2002, Men et al. 2003, Gouse et al. 2005, Wang et al. 2009, Berge and Ricroch 2010, Lu et al. 2010, Zhao et al. 2011, Wilson et al. 2013). The emergence of secondary pests potentially requires insecticide applications that can be detrimental to natural enemies and cause insecticide spray-associated pest outbreaks.

Significant pesticide reductions have been documented with adoption of Bt crops for cotton and sweet corn with smaller reductions for field maize (Cattaneo et al. 2006, Wu et al. 2008, Shelton 2010, Naranjo 2011, Brookes and Barfoot 2013, Shelton et al. 2013). These reductions are dependent upon region. A study reports that the reductions seen in the U.S. and Australia have not been maintained in China largely due to secondary pest outbreaks (Wang et al. 2009, Zhao et al. 2011). When insecticide reductions are achieved, natural enemy populations can be conserved to provide biological control of secondary pest populations as noted.

Regarding non-target arthropod effects outside of the agricultural setting (e.g., monarch butterfly, as discussed above), meaningful effects due to Bt crops have not materialized. This leaves two remaining hypothesized effects of Bt crops on in-field non-target natural enemy populations. One scenario envisioned a beneficial impact to natural enemies as broad-spectrum insecticide applications were reduced. Alternatively, natural enemies were predicted to decline due to the cumulative effects related to reduced prey quality or abundance of certain pest prey controlled by the Bt plant. For example, lepidopteran resistant Bt maize would control larvae soon after hatching, but egg masses and some young larvae would be available as prey for natural enemies. Additionally, regional suppression of a pest may occur resulting from long term and widespread planting of Bt maize.

There have been relatively few long-term field studies that could assess for the effects of cumulative subtle effects of prey removal on natural enemies, though results from existing studies and our experience with a long history of commercial Bt crops can

be reasonably extrapolated to the long term and large scale. However, persistent concerns require specific long term and landscape assessments (Meyer 2011). In a relatively long-term field study of Bt cotton over a period of six years, Naranjo (2005a) reported a reduction in five out of 22 foliar-dwelling natural enemies in Bt cotton relative to conventional cotton. However, they also found that the biological control function of the natural enemy communities in the Bt cotton and control on key pests was similar and lower for insecticide-treated plots (Naranjo 2005b). A long-term study conducted in China found that arthropod abundance increased and pest pressure decreased over the 10 years that Bt cotton compared to commonly insecticide treated conventional cotton (Lu et al. 2012).

Computer Simulation Models to Evaluate Non-target Organism Effects from Bt Crops

Relatively few studies have capitalized on approaches using computer model simulations for studying potential effects of Bt crops on non-target organisms. Computer simulations have often been used to study the development of resistance (Onstad et al. 1999, Crowder et al. 2006, Heuberger et al. 2011, Onstad et al. 2011, Kang et al. 2014, Desquilbet and Herrmann 2016, Pan et al. 2016) with some addressing the question of resistance delay due to biological control (Onstad et al. 2013). O'Rourke and Jones (2011) modeled the effect of pest management practice (e.g., Bt maize) and landscape diversity on pest population dynamics. Multiple studies by Sisterson and coauthors modeled the effects of the widespread planting of Bt crops on specialist parasitoids and potential effects on non-target organisms with implications for field study design

(Sisterson and Tabashnik 2005, Sisterson et al. 2007). Raybould et al. (2011) used the TrophicLINK model to simulate the effects on biological control when a natural enemy is sensitive to a hypothetical Bt protein and how the lost biological control was largely recovered with the addition of an insensitive natural enemy species. Given the difficulty of detecting effects of Bt crops in the field caused by potentially subtle indirect effects, a modeling approach may provide a good alternative to identifying key factors that can later be studied more specifically in the field. The case for this is furthered by Sisterson et al. (2007) questioning the validity of continued field studies in areas where arthropod communities have already be influenced by the widespread planting of Bt crops.

Extensive research has been conducted assessing for potential effects of Bt maize on non-target invertebrates, especially natural enemies. Although this work has not revealed unexpected non-target effects, the continued prevalence of research in the area highlights a considerable interest in understanding even subtle perturbations in the agroecosystem. This marks an important further transition from simply accepting the destruction of natural enemy populations caused by reliance on broad spectrum insecticides towards having a keen interest in more intimately understanding the role of natural enemies in the agroecosystem and how to conserve them. Additionally, a question inherent in this type of research is, “what effect is significant enough to cause a notable reduction to natural enemy populations?” The wealth of knowledge gained from the numerous studies conducted on potential non-target organism effects from Bt crops has not only demonstrated a lack of effects on non-target organisms, but also represents a

major contribution to our overall knowledge of pest and non-target organism biology in agriculture.

Objectives

Though the extensive research on Bt crops and natural enemies has not revealed unexpected non-target effects, these crops modify the agroecosystem by reducing the prey base available to natural enemies through removal of target pests. Though removal of pests is an intended result of this pest control measure, the change in the food web could lead to effects on natural enemies that utilize the removed pests as a food source. There are a number of key factors relevant to natural enemies that could be influential in mitigating or exacerbating the prey base reduction resulting from Bt crops. For example, if the prey reduction increases encounters between natural enemy individuals, the result could be increased cannibalism and intraguild predation. Alternatively, the potential effects of the prey reduction could be mitigated if the natural enemies are able to utilize other prey or non-prey food.

Thus, Bt crops offer a unique experimental scenario to study the response of natural enemies when only certain elements of the food web have been removed. The main objective of this research is to evaluate the effect of prey base reduction caused by Bt maize on natural enemies as well as the influence of cannibalism, intraguild predation, and utilization of alternative food resources in that context. Given the difficulty of studying these factors in the field, a food web model, TrophicLINK (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011), was modified to specifically simulate natural enemy,

pest, and maize interactions. The model is an individual-based model using aspects of functional ecology and food web network theory to simulate the trophic interactions of individuals and the resulting flow of energy (or biomass) (Caron-Lormier et al. 2009). The individual-based model approach emphasizes the unique experiences of individuals and their trophic interactions leading to system level effects, such as conservation of natural enemy populations, biological control, and maize yield.

The first part of the research focuses on the key factors of cannibalism, intraguild predation, and alternative food utilization in a conventional (non-Bt) maize scenario as a proof of concept test of the model and also to assess the influence of these factors independently of Bt maize. The second part of the research assesses the effect of prey reduction in a lepidopteran resistant Bt maize scenario on natural enemies. This objective includes a long-term Bt maize scenario where the target pest has been eliminated from the region, a short-term Bt maize scenario where adults, eggs, and young larvae remain, an insecticide-treated conventional maize scenario with all insects, a conventional untreated maize scenario consisting of pests alone, and a conventional untreated maize scenario consisting of both pests and natural enemies. The scenarios for both parts of the study will be assessed in terms of natural enemy abundance, pest suppression, and maize yield.

Given the importance of the agroecosystem and the additional demands that will be placed on the land by the growing world population, it is critical that we have tools to investigate not just the risk profile of changes in the agroecosystem, e.g., prey removal by Bt maize, but also how these changes interact within the existing complex array of crops,

agronomic practices, and management tools in the long term and landscape scale. This complexity precludes our ability to test all of these questions in the field; however, an efficient modeling approach could identify specific issues for consideration that can later be the focus of field studies.

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CHAPTER TWO

SIMULATING INTERACTIONS BETWEEN NATURAL ENEMIES AND PESTS IN MAIZE TO ASSESS THE INFLUENCE OF ALTERNATIVE FOOD, CANNIBALISM, AND INTRAGUILD PREDATION

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Manuscript Information Page

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Status of Manuscript:
__X__ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-review journal
____ Published in a peer review journal

CHAPTER TWO

SIMULATING INTERACTIONS BETWEEN NATURAL ENEMIES AND PESTS IN MAIZE TO ASSESS THE INFLUENCE OF ALTERNATIVE FOOD, CANNIBALISM, AND INTRAGUILD PREDATION

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Abstract

Natural enemies provide important biological control services in agroecosystems, but their ability to reduce pest populations and protect yield is highly variable. Here we use a model of the maize ecosystem to quantify biological control provided by natural enemies under conditions that contribute to variability of biological control, including utilization of maize pollen as an alternative food resource, cannibalism, and intraguild predation. An individual-based model was used to simulate interactions between maize, aphids, European corn borer, lady beetles, and lacewings. Natural enemies reduced a lepidopteran pest population by as much as 31%, which resulted in partial protection of maize yield. Pollen availability increased lady beetle and lacewing mean peak mass by 33 and 24%, respectively. Biological control by lady beetles was reduced in the presence of pollen, though this was not the case for lacewings, which had a lower affinity for pollen

as a food source. Cannibalism and intraguild predation reduced lady beetle and lacewing populations by 63 and 79%, respectively, but only small reductions in biological control levels resulted relative to scenarios without cannibalism and intraguild predation. Results demonstrate the importance of simulating multiple ecological interactions to better understand the role of natural enemies with respect to biological control and protection of yield in maize agroecosystems.

Introduction

The ecosystem service of biological control provided by natural enemies on agricultural pests is a major driver behind conserving natural enemy populations and a central tenet of Integrated Pest Management (IPM) (Stern et al. 1959, Kogan 1998). The ability of natural enemies to reduce pest populations—sometimes dramatically—has been well demonstrated (Symondson et al. 2002, Buteler et al. 2008, Naranjo and Ellsworth 2009, Obrycki et al. 2009), but the amount of biological control actually provided by natural enemies varies with respect to biological aspects of the species involved and interactions within and across species. Specific factors contributing towards variability in biological control include intraguild predation, cannibalism, and the utilization of alternative food by natural enemies. Our growing knowledge of the influence of these factors highlights the context-dependent nature of the degree of biological control provided by natural enemies (Straub et al. 2008, Tylianakis and Romo 2010), but isolating the effects of each is challenging in a field setting.

Although increasing natural enemy diversity often increases biological control (Snyder et al. 2006, Bruno and Cardinale 2008), it may also decrease (Finke and Denno 2004, Rosenheim et al. 2004, Finke and Denno 2005), or have no effect on prey suppression (Ives et al. 2005, Bruno and Cardinale 2008). The typical mechanisms associated with these scenarios include natural enemy competition, complementarity, and functional redundancy, respectively (Straub et al. 2008). One factor complicating biological control involving natural enemy competition is predation within and across natural enemy species. For instance, cannibalism may suppress natural enemy populations especially since some natural enemies, e.g., lady beetles (Coleoptera: Coccinellidae), often preferentially cannibalize eggs rather than feed on eggs of other natural enemy species (Agarwala and Dixon 1992, Dixon 2000). Cottrell and Yeargan (1998) found that adults and larvae of the lady beetle, *Coleomegilla maculata*, are the main predators of *C. maculata* egg clusters. However, predation of sibling eggs by lady beetles may benefit lady beetle populations when other prey are not prevalent (Agarwala 1991, Dixon 2000, Dixon and Kindlmann 2012). Likewise, larval cannibalism in the green lacewing, *Chrysoperla carnea* (Neuroptera: Chrysopidae), was found to be an adaptive trait when food was limiting (Duelli 1981) such that cannibalism plays an important ecological role as a food source that can both suppress and benefit natural enemy populations.

Intraguild predation (i.e., predation across natural enemy species) can also complicate the amount of biological control provided by natural enemies. The presence of a strong intraguild predator can reduce overall biological control in some systems

(Cisneros and Rosenheim 1997, Finke and Denno 2004, Rosenheim et al. 2004, Finke and Denno 2005). For example, Cisneros and Rosenheim (1997) investigated a system in cotton including the lacewing, *C. carnea*, a strong intraguild assassin bug predator, *Zelus renardii*, and a pest aphid, *Aphis gossypii*. The assassin bug alone was not able to suppress cotton aphid abundance; however, the lacewing could do so. When present, the assassin bug predated lacewings, which resulted in increased aphid abundance. In the absence of a strong intraguild predator, multiple natural enemy species may act in a complementary manner providing additive suppression of pests (Snyder et al. 2006, Bruno and Cardinale 2008). Despite these well-known examples of intraguild predation hindering prey suppression by a natural enemy community, other studies have found biological control to be unaffected by the presence of intraguild predators (Janssen et al. 2006).

The use of alternative food resources, including both breadth of prey items consumed and use of non-prey foods, is another factor adding complexity to the amount of biological control provided by natural enemies. Applying the term "predator" to a natural enemy in agriculture must consider its degree of omnivory (Lundgren 2009b) or, as discussed above, how the natural enemy interacts with other natural enemies. Generalist natural enemies able to colonize and survive in agro-ecosystems are extremely adaptable. The highly disturbed nature of annual agricultural systems inherently limits their biodiversity; however, certain natural enemies are well-adapted to such scenarios due to their ability to be highly vagile, polyphagous, effective at searching for prey, highly competitive, and to have high reproductive capacities (Wiedenmann and Smith

1997). Importantly, many natural enemies are resilient to unstable and disturbed environments in part by having flexible diets that include alternative prey and non-prey food resources including plant material, fungal spores, extrafloral nectaries, and honeydew deposits (Lundgren et al. 2005b, Lundgren 2009b, Lundgren 2009a, Lundgren et al. 2010, Choate and Lundgren 2013, Schmidt et al. 2013).

Utilization of pollen as a food resource by natural enemies is especially common in agriculture and has been documented for 37 predator species (Meissle et al. 2014). *Coleomegilla maculata* can complete development on pollen alone (Smith 1960, Lundgren and Wiedenmann 2004); and pollen can make up a significant portion of the diet of *C. maculata* (Lundgren et al. 2005b). Though larvae of *C. carnea* cannot typically complete development feeding on maize pollen alone, pollen may be an important supplement for lacewing larvae since most (58-87%) were able to reach pupation when one instar was fed pollen and the other two instars were fed an optimal diet of lepidopteran eggs (Meissle et al. 2014). In contrast to *C. maculata* adults that have similar feeding affinities as the immature stage, *C. carnea* adults are not predacious and their diet includes pollen (Li et al. 2010).

The utilization of alternative food resources by natural enemies could plausibly help or hinder biological control. For example, pollen in maize may attract natural enemies because it is a frequently utilized non-prey food source. Cottrell and Yeargan (1998) reported that *C. maculata* are more abundant in maize plots with pollen than in plots without pollen. However, the increased natural enemy abundance may not translate

to additional pest suppression since some natural enemies feed heavily on pollen to the detriment of biological control (Cottrell and Yeargan 1998, Musser and Shelton 2003b).

Cannibalism, intraguild predation, and alternative food resources can also interact to influence biological control (Cottrell and Yeargan 1998, Musser and Shelton 2003a). For example, *C. maculata* cannibalism was significantly lower in plots containing pollen as an alternative food resource (Cottrell and Yeargan 1998). Additionally, alternative prey utilization, such as aphids, can reduce biological control of a target pest (Musser and Shelton 2003b, a). Conversely, alternative prey may attract and sustain natural enemy populations allowing subsequent biological control of other pests (Michels and Matis 2008).

The factors discussed above and the variability they contribute to biological control highlight the need for context-specific data. Despite the obvious benefits of studying the effects of intraguild predation, cannibalism, and alternative food utilization on biological control of natural enemies under realistic field scenarios, isolating the effects of a particular variable and obtaining clear results can be difficult, expensive, and time-consuming. Likewise, aspects of reality are sacrificed when studying interactions in simplified laboratory systems, which may limit real world applicability. For example, most studies investigating intraguild predation were conducted in lab settings and, unsurprisingly, the results overstate the role of intraguild predation relative to more realistic studies (Weber and Lundgren 2009). Furthermore, biological control provided by natural enemies is variable based not only on the above factors but also across year, crop

type, species complex, and other variables. Thus, while conservation of natural enemies for biological control remains a valued goal of IPM, in many cases we lack specific knowledge of the contribution of biological control in pest suppression and the factors that affect it.

A food web modeling approach can apply what we know about multiple ecological interactions and combine them in different contexts to better understand their influence. In this respect, it would be possible to "tweak the strings" of the food web quickly and efficiently by varying key factors such as those discussed above to understand their role in biological control. The results of model simulations could then be assessed and applied to further modeling and/or applied to more focused field, greenhouse, or lab situations utilizing specific aspects highlighted by the simulations. Here, we use the food web individual-based model (IBM), TrophicLINK (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011) to simulate natural enemy, pest, and crop interactions in maize. Individual-based models emphasize bottom up processes where individual interactions collectively result in higher-level patterns, e.g., biological control. This model was modified to accommodate maize and to describe trophic interactions specific to a maize system in the Corn Belt of the United States. In this study, maize, natural enemies, and pests were modeled to better understand the influence of intraguild predation, cannibalism, and alternative food utilization on biocontrol services provided by natural enemies.

Methods

The TrophicLINK model (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011), written in C++ and compiled in Microsoft Visual Studio® (v. Community 2015), was developed to evaluate the role of trophic functional ecology on the diversity and dynamics of invertebrates and plants in agroecosystems. The model is individual-based, which entails tracking of individual organisms through their life cycle and through interactions with other individuals and their environment (Grimm et al. 2005). TrophicLINK was selected as a starting point for this effort because of the model's focus on individual variability and local trophic interactions influencing population level effects in agroecosystems. In addition, an individual-based model was considered important to capture potentially subtle population effects from various scenarios that might be lost without attention to the unique experiences of individuals. Modifications were made to the model to focus on above-ground trophic interactions of invertebrates and maize. A summary of the original model is provided here, with additional details given for modifications, following the standard IBM reporting guidance of Grimm et al. (2006). Additional model descriptions can be found in Caron-Lormier et al. 2009, 2011.

A general overview of the model includes the loading of input files describing the crop, invertebrates, environment, and population sizes. The model code guides the simulations based on functions, rules, and specific data from a set of input files relating to a scenario to be tested. The specified number of simulations are run and the resulting data

are written to output files for further analysis (Figure 2.1). Subsequent scenarios can then be loaded, run, and evaluated.

Purpose

The purpose of the modified TrophicLINK model is to simulate a portion of the maize ecosystem including the crop and natural enemy and pest invertebrates to evaluate the influence of alternative diet (i.e., maize pollen), intraguild predation, and cannibalism on natural enemy populations and their ability to provide biological control.

Entities, state variables, and scales

Organisms simulated are referred to as trophic-functional types since the interactions of interest are feeding interactions and the entity represented is less an individual species and more an aggregate of species that represent a "function" (i.e., herbivory, predation) based on similarity of life history and size (Caron-Lormier et al. 2009). Trophic-functional types include field maize, two pests (represented by corn leaf aphid, *Rhopalosiphum maidis* (Hemiptera: Aphididae) and European corn borer (ECB), *Ostrinia nubilalis* (Lepidoptera: Crambidae)) and two natural enemies (a lady beetle (Coleoptera: Coccinellidae) and green lacewing (Neuroptera: Chrysopidae)). Parameterization for the lady beetle is based most closely on *C. maculata* since this is a common lady beetle in maize in eastern North America (Conrad 1959, Musser et al. 2004). Parameterization of the green lacewing is based on *C. carnea*, also common in maize fields in the U.S. Corn Belt (Bruck and Lewis 1998).

Individuals follow typical life cycles, e.g., invertebrates start as eggs and progress through a larval stage, pupal stage (as applicable), adult stage, and then senescent adults. Populations are created and grow and individuals interact directly through feeding interactions and indirectly through competition for limited resources. State variables for individuals include a unique identification number, status as alive or dead, age, life stage, location (*x*- and *y*- coordinate in the simulated patch), and body mass.

Maize plants are partitioned into compartments, including stalk (or structure), the energy-producing portion of the plant (leaf), free store energy, propagule (seeds), and pollen. The maize plants progress through a period of vegetative growth followed by a reproductive stage when plants shunt energy towards both grain production and anthesis (i.e., pollen shed). Energy is apportioned to the different compartments based on the initial traits input values (Table 2.1). The inclusion of pollen shed was important in this model because maize pollen can be an important food source for natural enemies.

Invertebrate functional types consist of three compartments, including growth, reproduction (eggs), and free store energy. Energy derived from consumed food is used to grow (for immature invertebrates only), produce eggs, and maintenance (i.e., respiration). Invertebrates can feed on the plant in general or on specific plant tissues, on other invertebrates, or on both plant and invertebrates. There is no prey handling time for natural enemies based on the assumption that the time required to process prey items would be far shorter than the daily time step.

Habitat cells within the landscape are 5 m x 5 m and the habitat is homogeneous within that space. Temperature was simplified to be held at a constant 22 °C, which allowed for similar functional type development times of a fluctuating temperature regime. For example, the constant 22 °C temperature allows for 2600 growing degree days by day 120 of the simulated season which is equivalent to the growing degree days of the northern Corn Belt. Simulations were run for a 120-day maize growing season with a time step of one day.

Process overview and scheduling

At the outset of each simulation run, the 5 m x 5 m habitat cell is created and is further subdivided into micro-grid cells defined by the smallest foraging radius of the invertebrate functional types, which is 0.3 m. Cells are populated with crop plants uniformly established in rows according to input file values. Invertebrate individuals enter the simulation at a specified time step and randomly dispersed throughout the habitat cell with abundance based on input file values. At the start of each time step, individuals feed by progressing through the list of neighbors within their foraging radius in search of preferred food items. A feeding interaction occurs depending on a feeding preference tier matrix discussed further below under “submodels”. If food items are not present within an individual’s foraging radius and the individual remains sufficiently hungry, then that individual will pay an energy cost and disperse in search of food. An individual’s state variables are modified following interactions using asynchronous updating (i.e., each organism takes a turn independently as opposed to all feeding at

once). As such, food items that have been killed are removed from the model, which sets the stage for competitive interactions. No pest control applications are applied which is a realistic situation for field corn grown in the U.S. Corn Belt.

Energy obtained through feeding interactions is applied to growth for immature individuals and towards reproduction for adults. In this model, as with the original TrophicLINK model, all adult individuals are capable of reproduction. Offspring produced by adults enter the habitat cell as new individuals.

Two sources of mortality are included in the model. Mortality from predation is explicitly modeled as trophic functional types interact (or fail to interact when there is a shortage of food). Also, to maintain reasonable population levels, age-specific background mortality occurs based on a daily mortality rate provided by mortality input parameters.

Design concepts

The design concept metrics detailed below follow those from the standard guidance of reporting individual-based models, including basic principles, emergence, adaptation, objectives, prediction, sensing, interaction, stochasticity, collectives, and observation (Grimm et al. 2006).

The basic principles of the model are those processes that contribute to individual variability and govern trophic interactions. Individual variability is due to both variable life history trait input parameter values and from the unique experiences of individuals

based on spatial discrepancies, differential local resource availability and interactions, and a limited number of stochastic processes. Input data for life history traits can vary across individuals because data values are selected from a triangular distribution of a minimum, mode, and maximum values for each parameter. This is intended to allow for realistic natural variability for traits for which sufficient data exist. Areas where variability is important include pollen production and timing and invertebrate introduction timing. Variability for crop traits is minimized, aside from pollen production, to minimize noise that could potentially overwhelm effects of pests on crop yield and the ability of natural enemies to protect yield.

The objective of individuals is to survive and reproduce. Invertebrates interact with each other and plants, as applicable, during feeding interactions and indirectly through competition for limited food resources. Invertebrate population dynamics and crop yield emerge from individual behavior and the unique interactions of individuals. Certain elements of the model are stochastic including spatial placement of entering invertebrates, direction of dispersal of individuals, and background mortality. Invertebrate individuals can sense their own hunger level, food items within their foraging radius, and herbivores can indirectly sense competition from nearby individuals.

The only “collective” utilized in the model is an aphid colony which is simulated as a single entity, not as individuals. Aphids are modeled as colonies in the model because they are included simply as a food source mass for natural enemies and dynamics

of individual aphids are not a key element of the model. Adaptation of individuals, individual learning, and the ability of individuals to predict is not utilized by the model.

Simulation results are written to a general output file and a feeding mass matrix. The general output file includes data for each individual for each time step for identity, location, weights of the various compartments that comprise the organism, degree of hunger, and competition level. The feeding mass matrix output file reports the weight of material consumed for each trophic-functional type combination where interactions occurred.

Initialization

The model initiates with newly emerged maize plants in the 5 m x 5 m habitat cell. Additional trophic functional types are added at specific times (Table 2.2)

Input data

The model loads input files that can be modified from one set of simulations to the next to represent different scenarios. These files include environmental parameters, individual initial traits, and colonization timing (Table 2.1). Two additional input files are related to trophic interactions and are especially relevant to this effort. They include a matrix of functional types specifying food conversion efficiency and one for food preference tiers (Table 2.1). The environmental traits file includes general information about the simulation such as number of simulations, plot size, planting rate, etc., but also some parameters that apply broadly to multiple functional types (e.g., pollen degradation

rate). The initial traits file includes values related to the basic natural history of the organism, e.g., when does it enter the plot, how large is it at that time, what does it eat, developmental details, etc. Initial traits parameter descriptions are listed in Table A.1 with a complete list of values in Tables A.2-A.6. As described above, three values can be added for a parameter representing the minimum, mode, and maximum of values for a given parameter. Input values were obtained from the literature (direct parameterization) or determined by using reasonable values or by trial and error to obtain realistic results (inverse parameterization). No variability was added to a parameter if variable values were not available from the literature or if variability for that parameter was not of key interest. Values were converted to dry weight for plants and invertebrates to simplify modeling. The food conversion matrix input file is typically populated with values that represent the efficiency with which an organism utilizes the food it ingests for secondary production. In some cases, e.g., ECB, this value is based not on a conversion rate from the literature but is reduced to allow the feeding of ECB to a level of damage that approaches reality. Otherwise, it is difficult to simulate injury to the plant simply based on the large size and robust growth of the maize plant. The conversion rate values used are listed in Table A.7.

The food preference matrix contains values for the probability of feeding interactions between functional types (Table 2.1). Adults may maintain the same feeding preference as the immature stage (e.g., lady beetles) or may be assigned to not feed at all (e.g., ECB). The one exception includes lacewing adults that differ from the larval diet of aphids, pollen, cannibalism, and intraguild predation by feeding only on pollen and thus

differ from lady beetles in adult feeding. Adult moths that do not feed utilize an individual trait input that allows a portion of energy from the pupal stage for use in egg production. Food preference value assignments are listed in Table A.8.

Submodels

Figure 2.1 provides a flow diagram of the model including the subset of submodel processes used in TrophicLINK. The submodels of TrophicLINK are detailed in Caron-Lormier et al. (2011). Submodels utilized for the project include individual emergence, mortality, initial weight, foraging, dispersal, reproduction, growth, development, and respiration. Submodels developed and/or modified for this effort are described in Table 2.2. The addition of pollen production by plants was important because pollen is a key alternative food resource for many natural enemies. Another important change for this application was to separate the food conversion rate value from the determination of food preference, which was necessary for trophic interaction parameterization and results interpretation. To achieve this, a separate file contained the conversion rate value for each potential trophic-functional type combination and an additional file includes the probability that trophic-functional types will interact based on both a food preference tier value and hunger level (Table 2.1).

Simulation experiments

Testing and sensitivity analysis. Sensitivity analyses conducted by Caron-Lormier et al. (2011) included the following parameters: influence of juvenile mortality on plant weight and yield, herbivore feeding preference, and invertebrate foraging radius. Results of these analyses found the model behaving as expected and consistently. A parameter of interest for sensitivity analysis for this effort was daily pollen degradation rate, a parameter included in the environmental parameters input file. Evaluating different values for pollen degradation is important since pollen production is a new aspect of the model and pollen availability is subject to wide fluctuations in the environment. In addition, invertebrate foraging radius was again singled out as a parameter for sensitivity analysis given its clear importance in the ability of an individual to find food. Additional parameters were not tested since they are based on known aspects of functional types and are not subject to change without changing the nature of the functional type (e.g., characteristics like time to egg hatch, base weight, etc.).

Validation. A pattern-oriented approach to validation (Grimm et al. 2005) was used for the following patterns: maize growth and development, invertebrate growth and development, and population abundance. Validation results were assessed based on general concurrence of model and real-world data rather than exact matches.

Simulation scenarios. Scenarios were designed to test for the effect of pollen as an alternative food resource for natural enemies, intraguild predation (IGP), and cannibalism on the performance of natural enemies to affect pests (biological control), and maintain or

increase their own populations, and protect yield. Scenarios included (abbreviations in parentheses):

1. Maize with pollen, no pests or natural enemies (Maize alone)
2. Maize with pollen and pests (Pests only)
3. Maize with pollen + pests + natural enemies (All invertebrates + pollen)
4. Maize without pollen + pests + natural enemies (All invertebrates + no pollen)
5. Maize with pollen, pests, and natural enemies with IGP and cannibalism (All invertebrates + pollen + IGP + Can)
6. Maize without pollen, pests, and natural enemies with IGP and cannibalism (All invertebrates + no pollen + IGP + Can)

Twenty simulations were run for each scenario representing 20 different 5 x 5 m patches. The mass of pests and natural enemies, the mass of food items consumed by each invertebrate trophic functional type, and maize yield were evaluated for each scenario. The number of simulations selected was based on variability in maize yield (Fig. 2.2) and on having sufficient number of simulations to allow sampling of the triangular distribution of minimum, mode, and maximum parameter values for parameters. Relative differences across scenarios were assessed using mean values across simulations and 95% confidence intervals.

Results

Testing and Sensitivity

Testing. The variability of invertebrate trophic functional type mass over time using 20 simulations exhibits reasonably low variability for invertebrate functional types (Fig. 2.3).

Sensitivity. Figure 2.4 depicts the sensitivity analysis of maize pollen in terms of pollen mass over time and lady beetle mass over time while varying pollen degradation levels. Pollen levels and lady beetle mass over time show consistent decline as pollen degradation level drops. The effect of the amount of pollen on the mass of lady beetles, the trophic type with a high affinity for pollen, showed a decrease in response to decreasing food availability. Additionally, the selection of a 0.2 daily pollen degradation is supported as a sensible value. Variable foraging radius for natural enemies demonstrated that natural enemy population mass increased in a stepwise pattern as foraging radius increased and their prey, ECB and aphids, declined in the same manner as expected. (Fig. 2.5)

Validation results

Maize plant. The growth and development of the maize plant was modeled based on data from Dohleman and Long (2009) of approximately bi-weekly measurements of maize plant weights collected from a field in Illinois (F. Dohleman, personal communication). Physiological maturity of maize plants was on day 120 and at that time whole plant weight was 310 g and grain yield was 144 g dry weight. Maize pollen production was modeled to vary in a similar way as would be expected in a maize field including a variable start date and span of pollen flow for individual plants. The result of the parameterization related to pollen was temporally and spatially variable pollen production lasting for 14 days across the simulated patch with each plant shedding pollen from five to eight days (Purseglove 1972). Each plant produced a total of just over 1 g of pollen in total (Porter 1981); however, in the model it degrades by a 20% daily rate to mimic loss

of pollen due to environmental factors such as wind and rain. Parameterization of pollen results in initiation of pollen production by a few plants on day 57 (minimum parameter value), peak number of plants producing pollen on day 62 (mode parameter value), with the last plants producing pollen on day 66 (maximum parameter value). Thus, peak pollen mass occurs near day 65 at approximately 0.4 g of pollen per plant and declines from there rapidly until very little pollen is available by day 80.

Invertebrate functional types. The invertebrate functional types were parameterized to mimic patterns of growth and development of the actual insect. In some cases, direct parameterization was used (e.g., time as egg and time as pupa) or parameters were assigned values using reverse parameterization to obtain realistic results. An example of reverse parameterization was determination of values for development constant, food demand, and energy assigned to growth, which were parameterized in combination to yield an immature insect that grew to the appropriate weight in the appropriate amount of time. Key parameter values and growth and development results for ECB, lady beetle, and lacewing run under ideal conditions are presented in Table 2.3. The growth and development results in Table 2.3 are from simulations run under “non-stress” conditions with abundant food and no predation and so represent best-case values for the trophic functional types. Peak field abundance of Coccinellidae in maize varies considerably across studies, as would be expected, and includes approximate per plant values of 0.2, 0.3, 0.5, 0.6, 0.8, 1.1, 1.2, 1.5, 2, and 2.7 (Andow 1992, Pilcher et al. 1997, Dively et al. 2003, Musser et al. 2004, Park and Obrycki 2004, Ahmad et al. 2006). Peak abundance of the lady beetle functional type in these simulations ranges from approximately 1.9, 1.0,

0.6, 0.4, and 0.2 individuals per plant under ideal conditions (i.e., Table 2.3) and the all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + intraguild predation, and all invertebrates + no pollen + cannibalism + intraguild predation scenarios, respectively. Peak field abundance of lacewings in maize includes approximate per plant values of 0.1, 0.2, 1.5, 2.5 (Orr and Landis 1997, Pilcher et al. 1997, Bourguet et al. 2002, Dively et al. 2003, de la Poza et al. 2005). Peak abundance of the lacewing functional type in these simulations ranges from approximately 1.6, 1.0, 0.8, 0.2, and 0.2 individuals per plant under ideal conditions (i.e., Table 2.3) and the all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + intraguild predation, and all invertebrates + no pollen + cannibalism + intraguild predation scenarios, respectively.

Aphid colonies initiate from a single aphid entering the patch from day 40-46, grow to a maximum of 2.5 g and decline based on a daily degradation value of 0.12 which initiates when the colony becomes senescent after 43 days. This pattern of growth and decline of aphid colonies was selected to mimic typical aphid colonies in maize fields (Park and Obrycki 2004). Aphids were introduced into the plot at a rate of three aphids/ m^2 which resulted in 21% of plants infested with aphid colonies which agrees with Park and Obrycki (2004) who report approximately 20% of maize with aphids at Iowa field sites. As a result, aphids were sparsely populated in the plots and not immediately available as prey for natural enemies not in close proximity to aphids.

Simulation scenarios

The total mass of each invertebrate functional type is plotted over time for each scenario (Fig. 2.6). Aphid mass over time exhibits a small reduction of aphid peak population from the pests only scenario with the all invertebrate scenarios without pollen having the most reduction (Fig. 2.6a). Aphid mean peak mass was 193.2 g 95% [193.0, 193.5], 174.0 g 95% CI [173.2, 175.9], 157.8 g 95% CI [156.6, 160.0], 178.1 g 95% CI [176.5, 179.7], 163.0 g 95% CI [161.3, 164.7] for the pests only, all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + IGP, all invertebrates + pollen + cannibalism + IGP, respectively (Table 2.4). ECB mass over time declines from the pests only scenario to the scenarios including natural enemies (Fig. 2.6b). Mean peak ECB mass was 901.9 g 95% [894.5, 909.4], 639.5 g 95% CI [624.6, 654.4], 619.4 g 95% CI [609.1, 629.7], 681.9 g 95% CI [669.9, 694.0], 657.8 g 95% CI [639.1, 676.5] for the pests only, all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + IGP, and all invertebrates + no pollen + cannibalism + IGP, respectively (Table 2.4).

Lady beetle mass over time is highest in the all invertebrates + pollen scenario and declined in the absence of pollen, and inclusion of cannibalism, and IGP (Fig. 2.6c). Mean peak lady beetle mass was 2.7 g 95% CI [2.5, 2.8], 1.8 g 95% CI [1.6, 1.9], 1.0 g 95% CI [0.9, 1.1], 0.6 g 95% CI [0.5, 0.7] for the all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + IGP, and all invertebrates + no pollen + cannibalism + IGP, respectively (Table 2.4).

Lacewing mass over time was also highest in the all invertebrates + pollen scenario and declined in the absence of pollen, but was similar in cannibalism and IGP scenarios regardless of the presence of pollen (Fig. 2.6d). Mean peak lacewing mass was 2.9 g 95% CI [2.7, 3.2], 2.2 g 95% CI [2.1, 2.4], 0.6 g 95% CI [0.5, 0.6], 0.6 g 95% CI [0.5, 0.7] for the all invertebrates + pollen, all invertebrates + no pollen, all invertebrates + pollen + cannibalism + IGP, and all invertebrates + no pollen + cannibalism + IGP, respectively (Table 2.4).

The amount of food consumed by ECB and aphids is reported in Fig. 2.7. ECB consumes a much larger amount of maize plant compared to aphids. As expected, ECB consumption of maize plant corresponds to the pattern of ECB total mass with more plant consumed in scenarios that exhibited greater ECB mass (Figs. 2.6b, 2.7).

The amount of ECB consumed by lady beetles corresponds to the pattern of decline in ECB mass over time with lady beetles consuming the most ECB in all invertebrates + no pollen and incrementally less in all invertebrates + no pollen + cannibalism + IGP, all invertebrates + pollen, and all invertebrates + pollen + cannibalism + IGP, respectively (Figs. 2.6b, 2.8). Lacewing consumption of ECB shows a less distinct pattern, but the most ECB mass was consumed by natural enemies in the all invertebrates + pollen scenario (Fig. 2.8).

Both natural enemy populations were considerably reduced by the addition of cannibalism and IGP despite deprioritizing them as food items. Overall, cannibalism occurred much more frequently than IGP since individuals within a natural enemy

functional type were more frequently in close proximity than individuals across natural enemy functional types (Fig. 2.8). Values for cannibalism and IGP were generally higher for lady beetles than for lacewings (Fig. 2.8). Lady beetles also had higher cannibalism and IGP values when pollen was present (Fig. 2.8). As indicated by mean peak mass, pollen did not have as distinct an effect on cannibalism and IGP for lacewings (Fig. 2.8).

In terms of maize yield, the yield from the pests only scenario was reduced from a mean of 144.4 g to 115.7 g (Fig 2.7). Biological control provided by natural enemies resulted in some protection of yield with values ranging from 122.6 g from the all invertebrates + no pollen + Can + IGP to 124.7 g from the all invertebrates + no pollen scenario (Fig. 2.9).

Discussion

The model behaved as expected based on extensive testing, sensitivity analysis, and validation. Individuals interacted as expected based on food preference tier assignments, conversion rates, and certain rules including the size rule, protection from natural enemies of ECB larvae that have bored into the plant, and restriction of adult lacewings and ECB feeding. The realistic trophic functional type growth and development characteristics were reproduced by the model plus input values. Outputs addressing the same question from different directions (e.g., functional type mass over time, maize yield, predation mass) gave consistent results. The model was sensitive to varying pollen degradation levels and variable values for foraging radius, as expected.

Natural enemies reduced ECB populations by up to 31.3% in the all invertebrates + no pollen scenario which resulted in partial protection of maize yield. Reductions to ECB populations were caused by natural enemies feeding on ECB eggs and young larvae for the brief period when they were available before boring into the plant. Only small reductions to the aphid populations occurred since the colonies were well developed by the time the natural enemies entered the patches and the overall mass of aphids was difficult to affect by the relatively small mass of natural enemies. Suppression of the corn leaf aphids by coccinellids can be lacking (Foott and Timmins 1973) or inconsistent in maize based on a number of factors not least including protection from predation of aphid colonies because they are able to find refuge within the closed leaf whorl until the tassel is exposed prior to flowering (Elliott et al. 2002). As expected, predation of aphids increased in the absence of pollen.

Though maize yield was partially protected by scenarios including natural enemies, the small differences in yield across scenarios with natural enemies did not correspond well with the relatively large differences within natural enemy populations across scenarios. This discrepancy is related to the similarity in initial natural enemy egg loads across scenarios, low food preference value for cannibalism and IGP, and the limited amount of time that ECB eggs and larvae are available for predation. For example, regardless of scenario, natural enemy initial abundance was similar. The initial natural enemy larvae fed on potential food items depending on their affinity for a given food item. Cannibalism and IGP each have a low food preference (i.e., feed only two percent of the time regardless of hunger level or food upwards of 100% as hunger level

increases) and, as a result, natural enemies will only rarely feed on each other in the presence of other, more preferred food. Therefore, the initial focus of foraging natural enemies was largely on ECB, aphids, and pollen, if applicable, until preferred food items are depleted. The expectation for a situation including exposed foliar dwelling caterpillars is that the extended window for occurrence of predation would result in more separation between scenarios, though lepidopteran larvae would still not be subject to predation by these natural enemies once they are sufficiently large.

Lady beetle and lacewing populations were 33.0 and 24.1% higher in the presence of pollen, respectively. The results of these simulations agree with the findings of Cottrell and Yeargan (1998) that the population of a lady beetle that readily feeds on pollen was highest in maize plots with pollen and predation of a lepidopteran pest was lower per capita in the presence of pollen. Cottrell and Yeargan (1998) also reported lower cannibalism in plots containing pollen, which is consistent with simulation results initially, however, cannibalism ended higher in pollen scenarios since encounters of persisting lady beetles increased later in the season when other food was more sparse.

The simulations add an additional element of a natural enemy less reliant on pollen, the green lacewing. Though predation of ECB contrasted less across scenarios compared to lady beetle, the highest amount of ECB consumed by lacewings was in the all invertebrates + pollen scenario suggesting pollen did not reduce ECB predation for a natural enemy with less affinity for pollen. This indicates that natural enemies that utilize pollen to only “bridge the gap” when food is scarce are more likely to maintain or

increase levels of biological control in the presence of pollen in contrast to natural enemies that have a high affinity for pollen, such as *C. maculata*.

Lady beetle and lacewing mean peak mass was reduced by 63.0% and 79.3% in scenarios with pollen when cannibalism and IGP was included. Cannibalism occurred more frequently than IGP in the simulations. This occurred in the model not because of a difference in food preference setting between cannibalism and IGP but because individuals within the same natural enemy trophic functional type were more often in close proximity. It stands to reason that this would also be the case in reality, especially for young larvae originating from eggs laid in clusters. The amount of cannibalism and IGP also differed across the natural enemy trophic functional types. The amount of food consumed through cannibalism for lady beetles was higher compared to lacewings due to overall larger size of the lady beetle functional type and because they were active longer based on a shorter pupal period. Lacewings were more often victims of IGP from lady beetles rather vice versa because lacewings begin life smaller in size and the "size rule" favors larger individuals in these encounters; adult lady beetles also engage in both cannibalism and IGP, and lady beetles have a much shorter pupal period allowing them to be active in the patch while more food remains present. These findings contrast with laboratory IGP tests that find lacewings are more typically the stronger intraguild predator compared to lady beetle larvae of equal size likely due to the relatively large mandible size of lacewings (Michaud and Grant 2003, Noppe et al. 2012). Though laboratory IGP contest studies fill a need, the relevancy of the findings at the field level and on biological control has often been questioned (Costamagna et al. 2008, Weber and

Lundgren 2009). The model provides a middle ground intermediate in complexity between simple IGP contests and field level complexity. In these simulations, larvae of similar size and hunger levels are likely to win the IGP contest, but there are other layers of complexity influencing the overall outcome of intraguild predator encounters including presence of all life stages, extraguild food presence, the ability of individuals to disperse when food becomes sparse, and some degree of spatial heterogeneity.

The potential utility of the model is highlighted by the examples where the model can build on existing knowledge and explore mechanisms driving results as was the case with pollen effects. Additionally, the model could be easily modified to investigate similar systems. In the current study, pollen levels were simulated for field corn but sweet corn produces three to four times more pollen than field corn (Goss 1968, Nowakowski and Morse 1982). The model could easily investigate the role of pollen in that system where reduced insecticide sprays due to Bt maize would be expected to conserve natural enemy populations (Shelton et al. 2013). Also highlighted was the potential utility of the model to explore connections between existing types of studies, as was the case with IGP contest lab data and more complex plant level or field IGP evaluations.

Acknowledgments

The authors would like to acknowledge the following contributions to this project: F. Dohleman for providing maize plant growth measurement data; A. Martin and J. Uffman of Monsanto Company for rearing European corn borer and other insects to generate measurements used to support parameterization; G. Caron-Lormier for his

support in understanding of TrophicLink and making initial modifications to the model, and, lastly, a debt of gratitude is owed to scientists that have contributed to the extensive body of literature relied on to parameterize the model.

Table 2.1. Model input file descriptions

Input file	Input file description
Environmental parameters	Environmental parameters define the plot and other aspects that apply broadly; including number of simulations, length of simulation, temperature, plot size, planting density, and pollen decay rate.
Initial traits	Basic natural history aspects of individuals. See list of initial traits in Table 2 and specific values for the different trophic-functional types in Table 3).
Colonization	The initial entry into the plot is an initial trait; however, individuals can enter later during any time step and at any abundance using the colonization file.
Conversion rate matrix	The efficiency with which an individual converts the food it consumes to growth and/or reproductive mass is entered in this file as a ratio. For example, a lepidopteran larva may convert 20% of the plant tissue it consumes to growth.
Food preference tier matrix	This file is a matrix of functional types containing values that represent the probability that of one functional type feeding on another. Tiers are as follows: No interaction occurs (tier 5), an individual will feed on the item encountered up to 50% of the time depending on its level of hunger (tier 4), an individual will minimally feed on the item encountered up to 2% of the time increasing to 100% of the time as hunger increases (tier 3), an individual will minimally feed on the item encountered 30% of the time increasing to 100% of the time as hunger increases (tier 2), always feed if encountered (tier 1).
Managements	The managements file includes information describing the effects of a disturbance, such as an insecticide spray. Values determine when a disturbance occurs and how often, what functional types it effects and to what extent it effects different life stages, and how long a given disturbance continues to effect individuals.

Table 2.2. Modifications made to the TrophicLINK model for this project

Model Modification	**Description**
Pollen production	Pollen was a key change for this project since it is an important alternative food resource for many natural enemies. Plants were enabled to use a portion of their energy to produce pollen for a given amount of time. A pollination initiation time was added to allow for variable pollination start across plants.
Super aphid	Tracking extremely large numbers of individuals is computationally expensive and requires very long simulation times. Aphids quickly become abundant (e.g., into the millions) and cause run times to stretch into days. A super aphid individual was created since individual aphid dynamics is not a key aspect of the project. The importance of the presence of aphids is to provide a sporadically located food resource mass for natural enemies. A super aphid individual simultaneously grows and reproduces, is associated with a single plant when/if it successfully locates a host, and the population declines once it becomes senescent.
Stalk borer	Stalk borers, such as the European corn borer, are protected from predation once they bore into the plant one day after egg hatch. Borers are available to natural enemies as a food resource only during the egg stage and for a day after egg hatch.
Predation size rule	Natural enemies are limited in their ability to attack prey that are unrealistically large for them to handle. They cannot feed on prey larger than two times their own body weight.
Food preference tiers	TrophicLINK initially had an interaction matrix input file including food preference linked with conversion rate. These two aspects of feeding were decoupled to allow for modification of food preference without having to scale the conversion rate. Specific food preference tiers are described in Table 1.
Adult food preference	Adult invertebrates are enabled to have different food preferences than the immature stage. Examples where this is applied is for adult lepidopterans to not feed and allowing adult green lacewings to feed on pollen according to their realistic food preference. Lacewing adults also feed on aphids in order for them to survive and oviposit in scenarios without pollen.
Consumption Mass Output	An additional output file was added to report the amount of a given food item that a trophic-functional type consumed. This is referred to as predation mass within the code.

Table 2.3. Key parameter values and growth and development outcomes under ideal conditions for the ECB, lady beetle, and lacewing trophic functional types[1]

Characteristic	ECB	Lady Beetle	Lacewing
Initial abundance (per m^2)	3	0.5	0.5
Entrance day[2]	58; 60, 64, 68	60; 60, 63, 66	60; 60, 63, 66
Max initial egg load (# eggs/5x5 m patch)[3]	2538	793	720
Single egg weight (mg)	0.01	0.052	0.022
Time to egg hatch (days)	4	4	5
Larval development time (days)[4]	16	12	12
Foraging radius (m)	0.5	0.3	0.3
Pupal stage (days)[5]	N/A	7	15
Maximum weight of larva (g) [4]	0.119	0.012	0.09
Peak population mass (g)	901.9 (15.9)	5.4 (0.2)	4.5 (0.4)

[1] Key aspects of the remaining trophic functional type, aphids, are described in the methods because aphids are not modeled as individuals. Max initial egg load, larval development time, and peak mass represent "Ideal conditions", i.e., abundance of a preferred food type and no predation.
[2] The first number is entered in the colonization input file and the second set represents the minimum, mode, and maximum values of the initial abundance parameters from the initial traits input file.
[3] Total eggs deposited by initial adults
[4] Larval development time and maximum weight outcomes are the result of the combined parameter values of developmental constant, food demand, and energy to growth. The larval development is delayed when individuals are not able to acquire sufficient food.
[5] ECB were assumed to overwinter as pupae so second generation adults were not included in the simulation.

Table 2.4. Mean peak mass of the herbivore and natural enemy trophic functional types from each scenario[1]

Invert Functional Type	Scenario				
	Pests only	All inverts, pollen	All inverts, no pollen	All inverts, pollen,Can,IGP	All inverts, no pollen,Can,IGP
Aphid	193.2 g (193.0, 193.5)	174 g (173.2, 175.9)	157.8 g (156.6, 160.0)	178.1 g (176.5, 179.7)	163.0 g (161.3, 164.7)
ECB	901.9 g (894.5, 909.4)	639.5 g (624.6, 654.4)	619.4 g (609.1, 629.7)	681.9 g (669.9, 694.0)	657.8 g (639.1, 676.5)
Lady beetle	n/a	2.7 g (2.5, 2.8)	1.8 g (1.6, 1.9)	1.0 g (0.9, 1.1)	0.6 g (0.5, 0.7)
Lacewing	n/a	2.9 g (2.7, 3.2)	2.2 g (2.1, 2.4)	0.6 g (0.5, 0.6)	0.6 g (0.5, 0.7)

n/a indicates that the invertebrate trophic functional type was not included in that scenario
[1]Mean peak dry matter per 5 x 5 m patch (95% CI lower limit, 95% CI upper limit)

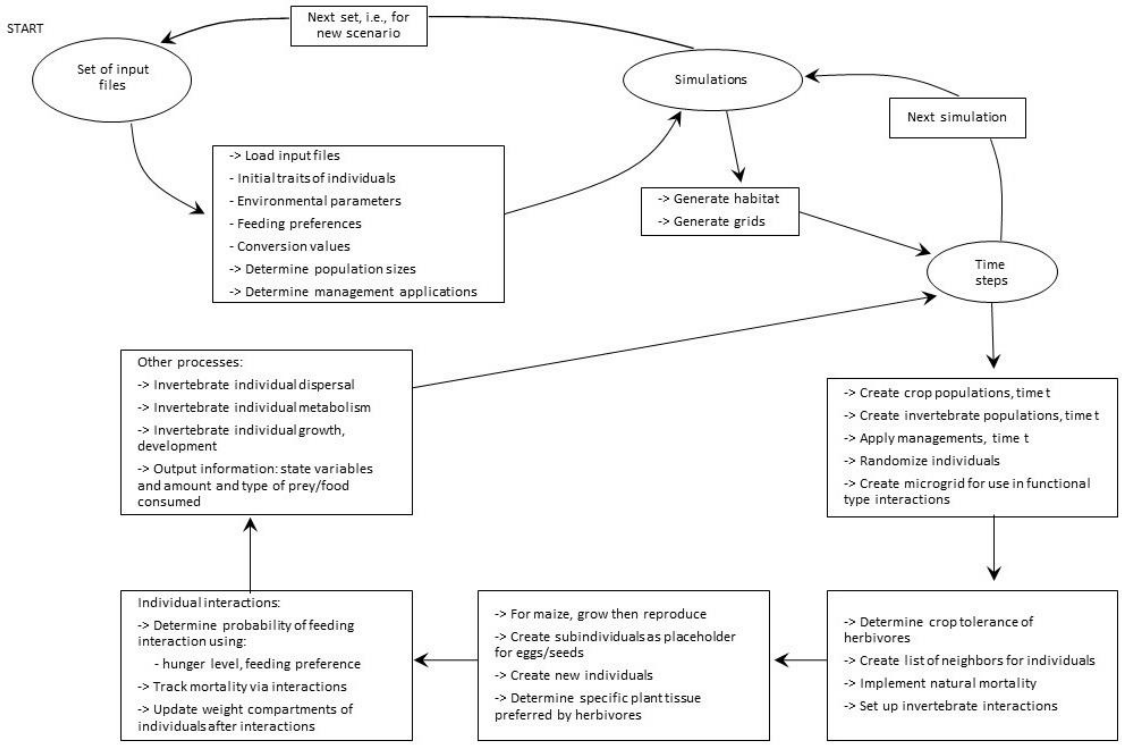

Figure 2.1. Flow diagram of the model. Modified from Caron-Lormier et al. (2011)

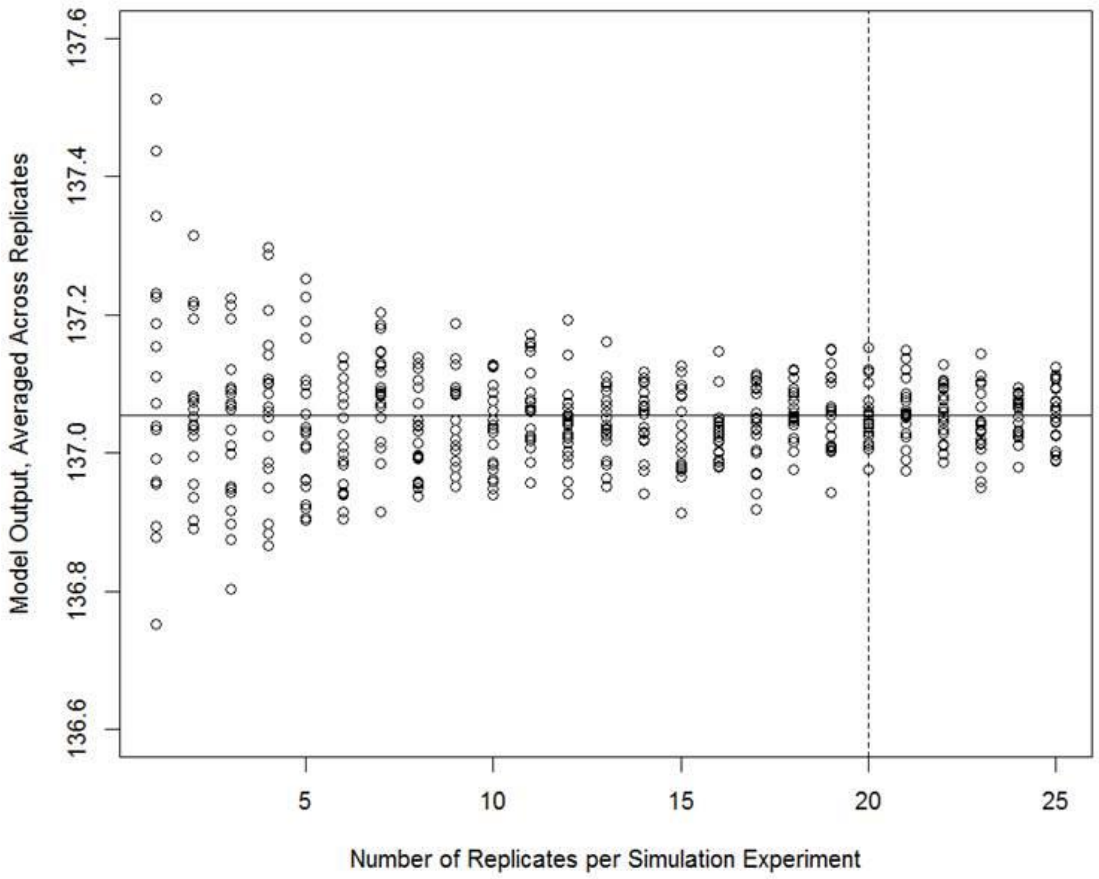

Figure 2.2. Maize yield variability depending on simulation number. The line represents the number of simulations selected to run for each scenario.

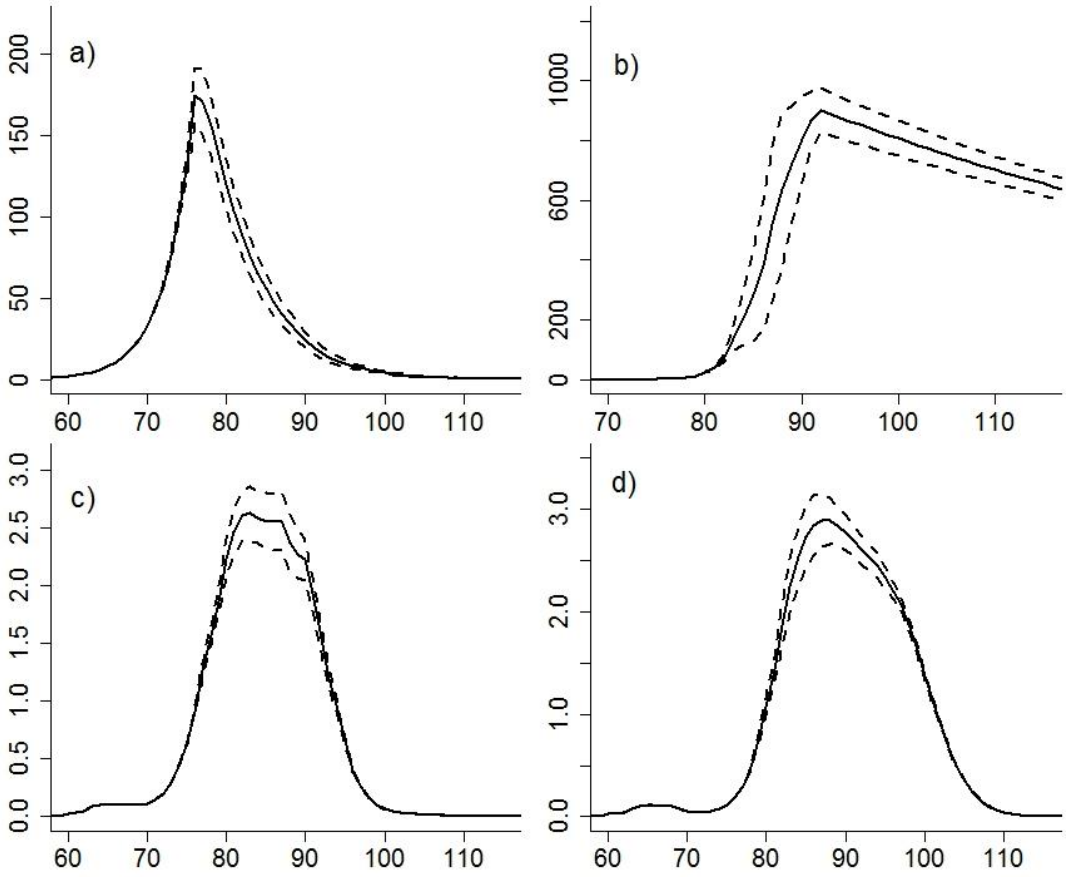

Figure 2.3. Variability of a) aphid, b) European corn borer, c) lady beetle, d) lacewing trophic functional type mass (g) over time with data combined from 20 simulations of a 120-day season. x-axis = day of growing period; y-axis = total dry matter production per 5 x 5 m patch.

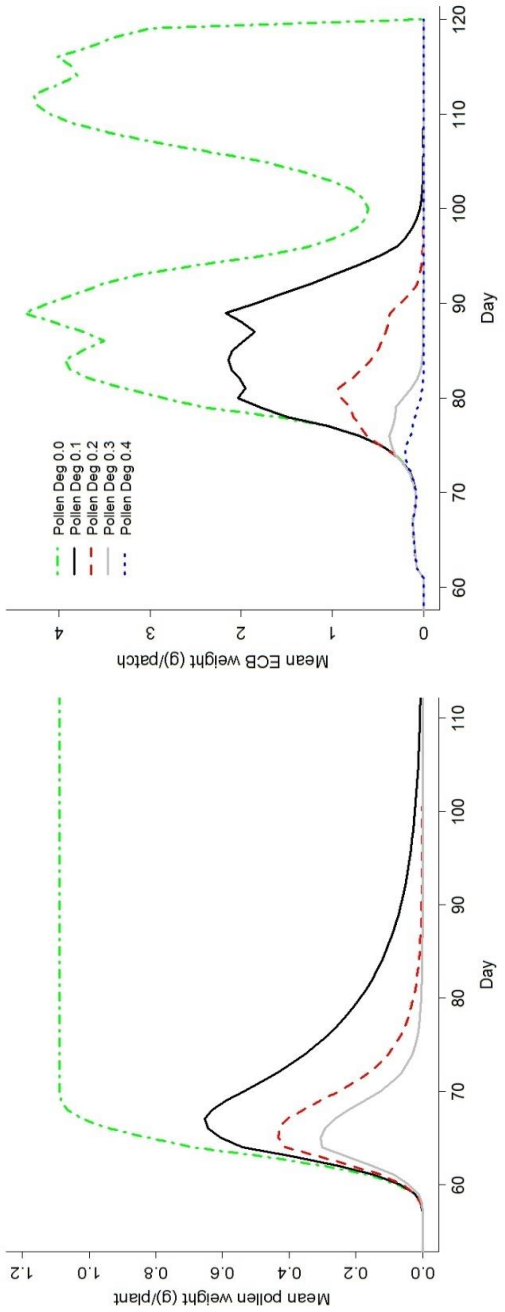

Figure 2.4. Effects of varying daily pollen degradation rates on pollen amounts over time (left) and on lady beetle mass over time (right). The pollen degradation rate of 0.2 was selected for simulation scenarios.

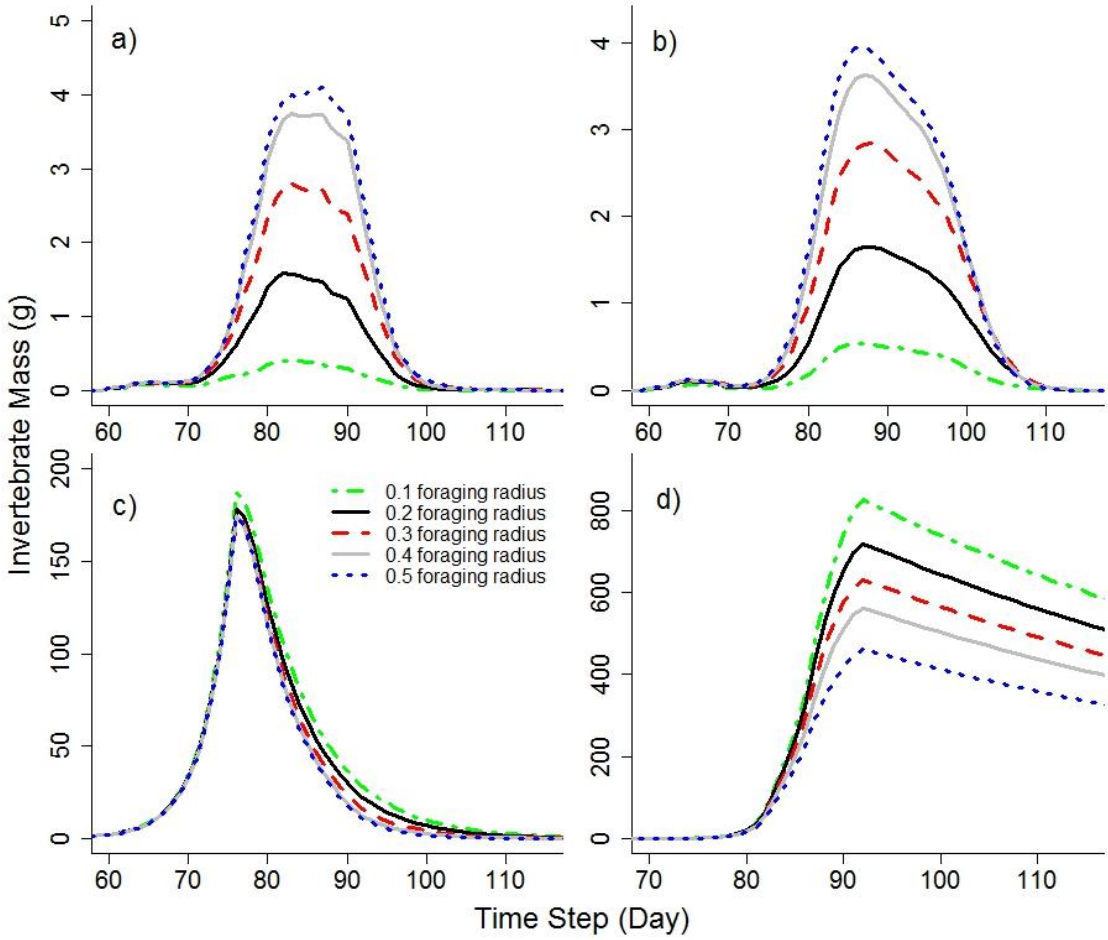

Figure 2.5. Invertebrate trophic type mass across the season with foraging radius values varied for a) lady beetle and b) lacewing and resulting prey mass of c) aphids and d) European corn borer. Foraging radius for lady beetle and lacewing individuals varied from 0.1 m, 0.2 m, 0.3 m, 0.4 m, and 0.5 m.

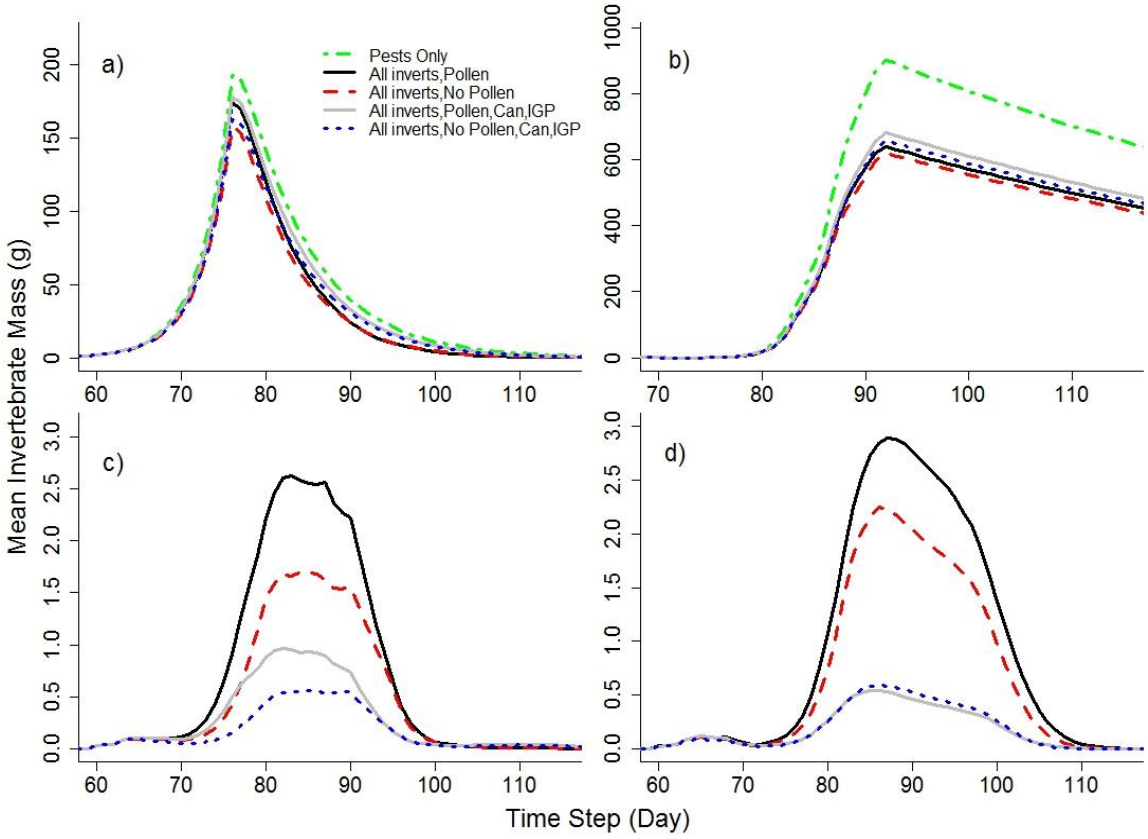

Figure 2.6. Invertebrate trophic type mass across the season for each scenario for a) aphid, b) European corn borer, c) lady beetle, and d) lacewing. Scenarios include pests only; all invertebrates, pollen; all invertebrates, no pollen; all invertebrates, pollen, cannibalism, intraguild predation; and all invertebrates, no pollen, cannibalism, intraguild predation.

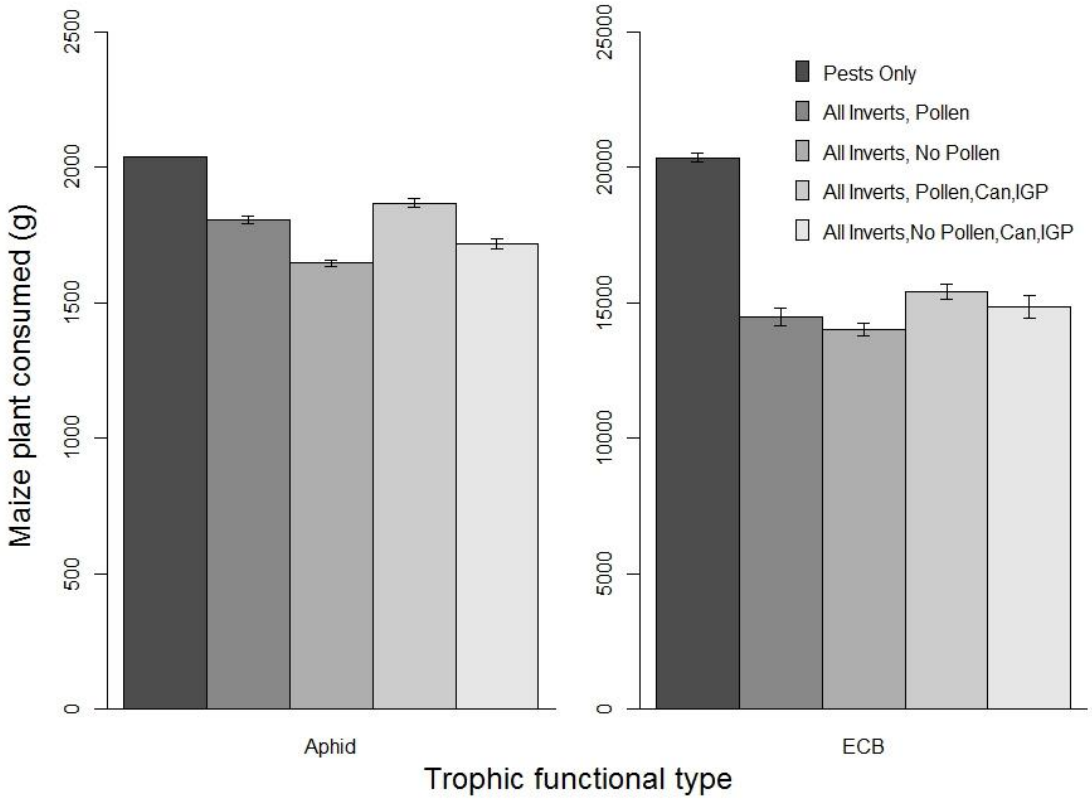

Figure 2.7. The amount of maize plant consumed by the herbivore trophic types, European corn borer (ECB) and aphid for different TrophicLINK simulations.

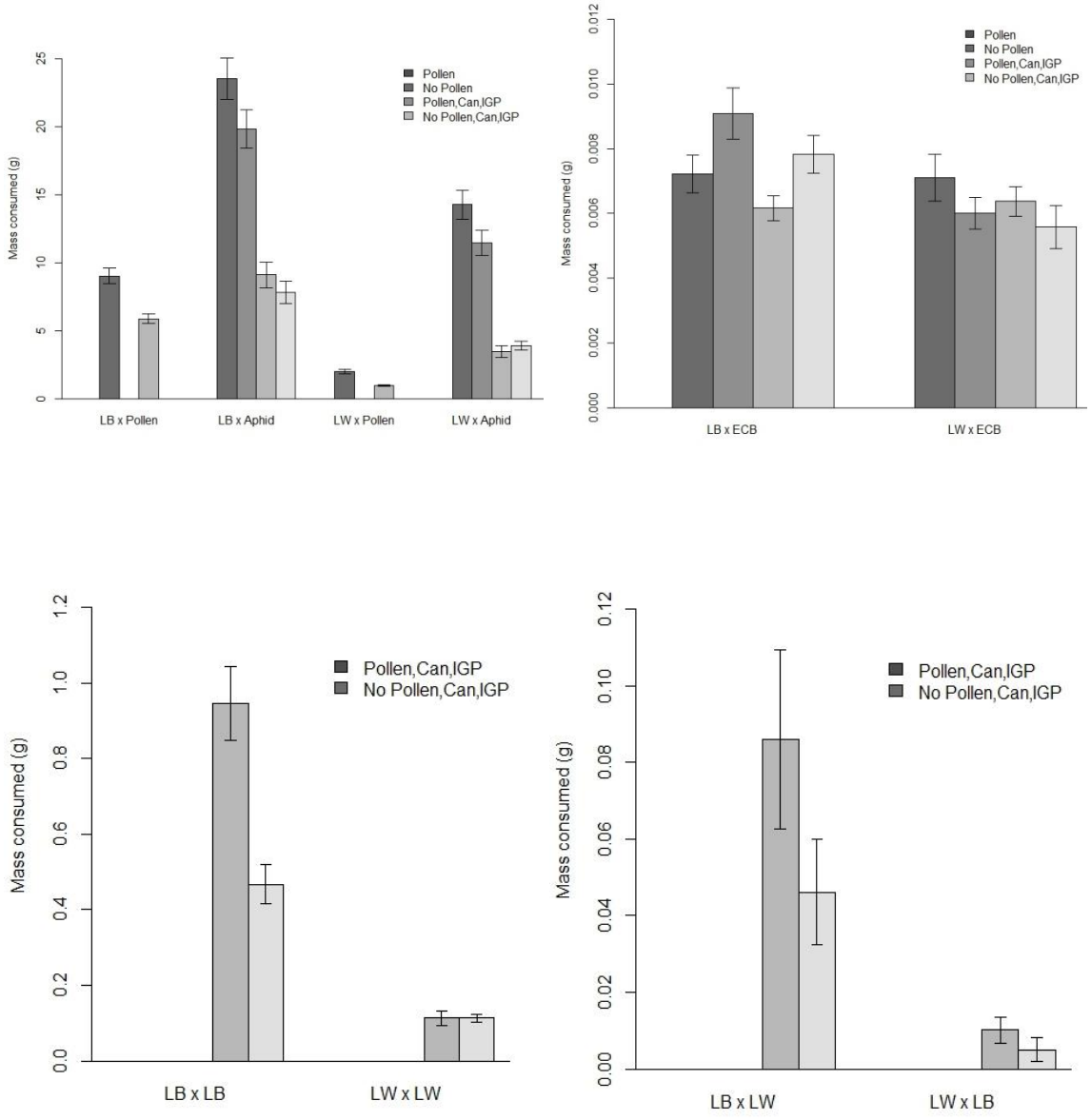

Figure 2.8. Amount of food consumed in each trophic interaction combination. Feeding interactions are labeled on the x axis as "feeder x consumed". LB= lady beetle, LW= lacewing. Note the different scale of the cannibalism simulations (left) versus the intraguild predation (IGP) simulations (right).

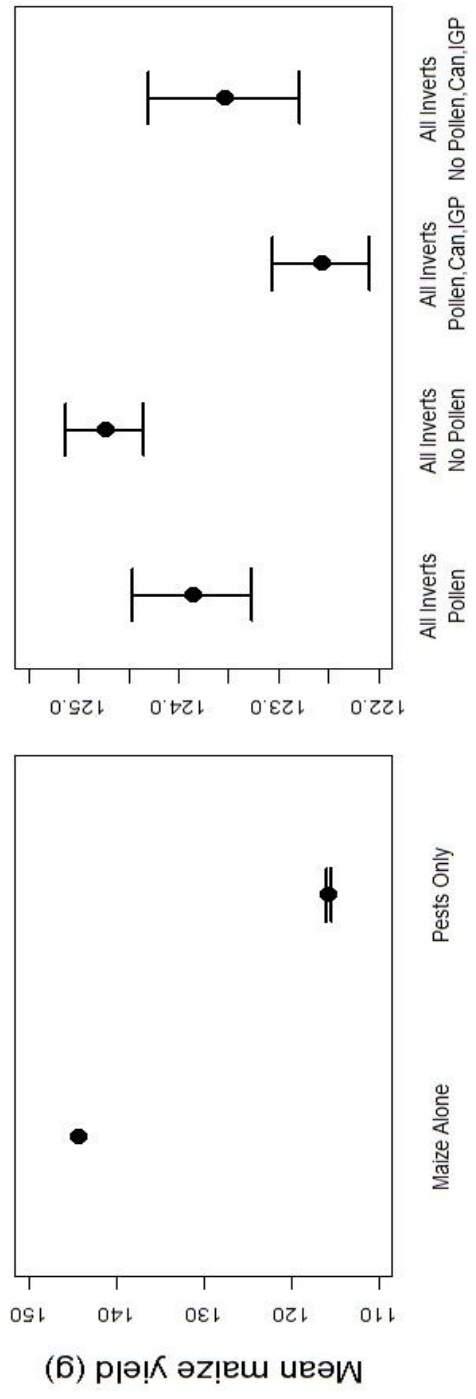

Figure 2.9. Maize yield across scenarios. Presented as means with 95% confidence intervals.

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CHAPTER THREE

SIMULATING INTERACTIONS BETWEEN NATURAL ENEMIES AND PREY IN BT AND CONVENTIONAL MAIZE

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Manuscript Information Page

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Status of Manuscript:
__X__ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-review journal
____ Published in a peer review journal

CHAPTER THREE

SIMULATING INTERACTIONS BETWEEN NATURAL ENEMIES AND PREY IN BT AND CONVENTIONAL MAIZE

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Abstract

Maize, *Zea mays*, and other crops have been genetically modified to produce proteins from *Bacillus thuringiensis* (Bt) that control certain insect pests. As target pests feed on the crop and are killed by the Bt proteins, they are removed from the system and are subsequently not available as prey items to sustain natural enemies. The removal of prey could negatively affect natural enemies and the ecosystem services they provide. The result of prey removal on natural enemies was simulated using an individual-based model involving maize; a non-susceptible pest, aphids; a susceptible pest, European corn borer; and two generalist predators, a lady beetle and green lacewing. Prey-reduced scenarios included a short-term Bt maize scenario that included ECB eggs and young larvae, and a second scenario without any ECB representing regional suppression of ECB over time by wide adoption of the Bt maize. The mass of lady beetle and green lacewings

was similar across scenarios except for the insecticide scenario, which reduced natural enemy mass by 65 and 78% percent, respectively. The findings support resiliency of generalist natural enemies to prey removal in the scenarios simulated.

Introduction

The potential for environmental effects of genetically modified crops has been a major concern since their introduction in 1996 (Peterson et al. 2000, Dale et al. 2002, Nicolia et al. 2014). One area of particular concern is the potential effects to natural enemies from genetically modified crops that produce proteins from *Bacillus thuringiensis* (Bt) to manage certain pests (Obrycki et al. 2001, O'Callaghan et al. 2005, Gatehouse et al. 2011). Extensive research has been conducted characterizing effects of Bt crops on non-target invertebrates, especially natural enemies (Naranjo 2005b, O'Callaghan et al. 2005, Duan et al. 2008b, Romeis et al. 2009, Carstens et al. 2012, Devos et al. 2012). Although this work has not revealed unexpected non-target effects, the continued prevalence of research in the area highlights a considerable interest in understanding even subtle perturbations in agroecosystems.

Although recognizing challenges associated with Bt crops and other pest control measures, e.g., resistance and secondary pest outbreaks, Bt crops potentially enable a shift from managing natural enemies where broad-spectrum insecticides are the norm to one where insecticide sprays are minimized. The Bt proteins expressed by the genetically modified crops currently in use exhibit restricted insecticidal activity spectra allowing for the management of certain pests while leaving the remainder of the invertebrate

community largely intact. Thus, Bt crops offer a unique experimental situation where only certain elements of the food web have been removed, which creates the opportunity to study the effects of these changes on natural enemies.

In the case of Bt maize, *Zea mays*, indirect effects on natural enemies may occur due to a reduced prey abundance caused by the desired effect of pest control by the Bt plant (Obrycki et al. 2001, Schuler et al. 2005). For example, lepidopteran-resistant Bt maize controls pest larvae soon after they hatch and initiate feeding, but egg masses and some young larvae would be available as prey for natural enemies. Prey abundance is further reduced when regional suppression of a pest occurs due to high adoption rates of a Bt crop on a regional scale. Regional suppression results in further reduction of prey abundance for natural enemies because the adult pests are no longer present to oviposit thus removing eggs and small larvae. Regional suppression of a pest due to high adoption of Bt crops has been documented in the U.S. in Bt cotton, *Gossypium hirsutum*, and Bt maize. Pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae) and the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae) have been regionally suppressed through high adoption of Bt cotton and Bt maize, respectively (Carriere et al. 2003, Wu et al. 2008, Hutchison et al. 2010).

Results from field studies have not shown adverse effects of Bt crops on generalist natural enemies (Dively et al. 2003, Bhatti et al. 2005a, Daly and Buntin 2005, Ahmad et al. 2006, Rauschen et al. 2010a, Comas et al. 2014). This is in line with Obrycki et al. (2001) who suggest that generalist predators might be able to manage

reduction in pest prey by switching to alternative prey. The ability of generalist natural enemies to thrive in the disturbed agroecosystems requires this kind of flexibility, however it stands to reason that there are limits in their tolerance of prey reduction.

Few studies have investigated prey reduction tolerance in multitrophic systems with genetically modified crops with the exception of Schuler et al. (2005), who infested nontransgenic and Bt oilseed rape, *Brassica napus*, plants with a highly susceptible lepidopteran, a non-susceptible aphid at varying levels, and a lacewing predator. No differences were found between the abundance and weight of lacewing predators recovered from plants at the highest aphid infestation level, however lacewings were significantly affected at the lower infestation levels of aphids (Schuler et al. 2005). These results indicate that natural enemies may be tolerant to prey reduction, though there are limits below which they may be negatively affected. Despite the obvious benefits of studying the effects of Bt maize and prey reduction on biological control of natural enemies under realistic field scenarios, isolating the effects of a particular variable and getting clear results can be difficult, expensive, and time-consuming. In addition, abiotic effects can overwhelm the potentially minor effects of natural enemy interactions with each other, their prey, and alternative food resources (Peterson et al. 2009). Though potentially subtle effects can be difficult to study at the field level, more controlled experiments enable evaluation of specific problems in the absence of overwhelming environmental variability. There currently exists an abundance of laboratory data demonstrating the occurrence of prey-mediated effects to natural enemies caused by a reduction in quality of susceptible or partially susceptible prey that have fed on a diet or

plant tissue including Bt proteins (Dutton et al. 2002, 2003, Schuler et al. 2004, Dutton et al. 2005, Ferry et al. 2006, Sanders et al. 2007, de Jesus et al. 2014). At the other end of the spectrum of study complexity, an abundance of Bt crop field data demonstrates a lack of consistent effects on natural enemies as discussed above. Studies of intermediate complexity could help to bridge the gap of lab and field results.

As part of a multi-pronged approach to increase understanding of indirect effects of Bt maize not easily discerned in natural environments, this effort uses a modeling approach as middle ground between the simplicity and predictability of laboratory toxicity testing and field level complexity. The TrophicLINK model (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011) was modified (see Chapter 2) to simulate interactions between Bt maize, pest, and natural enemy interactions to allow for scrutiny of a variety of life history parameters related to prey removal. TrophicLink is an individual-based model using aspects of functional ecology and food web network theory to simulate the trophic interactions of individuals and the resulting flow of energy (or biomass). The individual-based model approach emphasizes the unique experiences of individuals and their trophic interactions leading to system level effects, such as conservation of natural enemy populations, biological control, and maize yield. A food web modeling approach takes what we know about the system and applies it in different contexts (scenarios) to better understand the influence of various factors. In this respect, it would be possible to "tweak the strings" of the food web quickly and efficiently by varying key factors such as those discussed above. The results of model simulations could then be assessed and applied to further modeling and/or applied to more focused

field, greenhouse, or lab situations utilizing specific aspects highlighted by the simulations. Individual-based modeling puts an emphasis on bottom up processes where individual interactions collectively result in higher level patterns, e.g., biological control. The TrophicLink model was modified (see Chapter 2) to accommodate maize and simulate more specific aspects of trophic interactions. In this study, maize, natural enemies, and pests were modeled to better understand the influence of Bt maize and prey removal on natural enemy populations and biological control services they provide.

Methods

The TrophicLINK model (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011), written in C++ and compiled in Microsoft Visual Studio® (v. Community 2015), was developed to evaluate the role of trophic functional ecology on the diversity and dynamics of invertebrates and plants in agroecosystems. The model is individual-based which entails tracking individual organisms through their life cycle and through interactions with other individuals and their environment (Grimm et al. 2005). TrophicLINK was used because of the model's focus on individual variability and local trophic interactions influencing population level effects in an agroecosystem. In addition, an individual-based model was considered important to capture potentially subtle population effects from various scenarios that might be lost without attention to the unique experiences of individuals. TrophicLINK was modified in Chapter 2 to focus on above-ground trophic interactions between invertebrates and maize. A brief summary of the model is provided here following the standard IBM reporting guidance of Grimm et

al. (2006). Additional model descriptions can be found in Caron-Lormier et al. (2009, 2011) and Chapter 2.

Purpose

The purpose of the modified TrophicLINK model is to simulate a portion of the maize ecosystem including the crop and natural enemy and pest invertebrates to evaluate the influence of prey removal due to Bt maize on natural enemy populations and their ability to provide biological control.

Entities, state variables, and scales

Organisms simulated are referred to as trophic-functional types since the interactions of interest are feeding interactions and the entity represented is less an individual species and more an aggregate of species that represent a "function" (i.e., herbivory, predation) based on similarity of life history and size (Caron-Lormier et al. 2009). Trophic-functional types include field maize, two pests, represented by corn leaf aphid, *Rhopalosiphum maidis* (Hemiptera: Aphididae) and European corn borer (ECB), *Ostrinia nubilalis* (Lepidoptera: Crambidae), and two natural enemies, a lady beetle (Coleoptera: Coccinellidae) and green lacewing (Neuroptera: Chrysopidae). Parameterization for the lady beetle is based most closely on *Coleomegilla maculata* because this is a common lady beetle in maize in the U.S. Corn Belt (Conrad 1959, Musser et al. 2004). Parameterization of the green lacewing is based on *Chrysoperla carnea*, also common in maize in the U.S. Corn Belt (Bruck and Lewis 1998).

Individuals follow typical life cycles, e.g., invertebrates start as eggs and progress through a larval stage, pupal stage (as applicable), adult stage, and then senescent adults. Populations are created and grow and individuals interact directly through feeding interactions and indirectly through competition for limited resources. State variables for individuals include a unique identification number, status as alive or dead, age, life stage, location (*x*- and *y*- coordinate), and body mass.

Maize plants are partitioned into compartments, including stalk (or structure), the energy producing portion of the plant (leaf), free store energy, propagule (seeds), and pollen. The maize plants progress through a period of vegetative growth followed by a reproductive stage when plants shunt energy towards both grain production and anthesis (i.e., pollen shed). Energy is apportioned to the different compartments based on the initial traits input values. Pollen shed is included because pollen can be an important food source for some natural enemies.

Invertebrate functional types consist of three compartments, including growth, reproduction (eggs), and free store energy. Energy derived from consumed food is used to grow (for immature invertebrates only), produce eggs, and maintenance (i.e., respiration). Invertebrates can feed on the plant in general or on specific plant tissues, on other invertebrates, or on both plant and invertebrates. There is no prey handling time for natural enemies based on the assumption that the time required to process prey items would be far shorter than the daily time step.

Habitat cells within the landscape are 5 m x 5 m and the habitat is homogeneous within that space. Temperature was simplified to be held at a constant 22 ºC which allowed for similar functional type development times of a fluctuating temperature regime. For example, the constant 22 °C temperature allows for 2600 growing degree days by day 120 of the simulated season which is equivalent to the growing degree days of the northern U.S. Corn Belt. Simulations run for a 120-day maize growing season and a time step represents one day.

Process overview and scheduling

At the outset of each simulation run, the 5 m x 5 m habitat cell is created and is further subdivided into micro-grid cells defined by the smallest foraging radius of the invertebrate functional types, which is 0.3 m. Cells are populated with crop plants uniformly established in rows according to input file values. Invertebrate individuals enter the simulation at a specified time step and abundance based on input file values and are randomly dispersed throughout the habitat cell. At the start of each time step, individuals feed by progressing through the list of neighbors within their foraging radius in search of preferred food items. A feeding interaction occurs depending on a feeding preference assignments discussed further below under “submodels”. If food items are not present within an individual’s foraging radius and the individual remains sufficiently hungry, then that individual will pay an energy cost and disperse in search of food. An individual’s state variables are modified following interactions using asynchronous updating (i.e., each organism takes a turn independently as opposed to all feeding at

once). As such, food items that have been killed are removed from the model which sets the stage for competitive interactions. One scenario tested includes an insecticide application to manage the ECB trophic functional type which is occasionally necessary in field corn grown in the upper Midwest (Mason et al 1996).

Energy obtained through feeding interactions is applied to growth for immature individuals and towards reproduction for adults. All adult individuals are capable of reproduction and offspring produced by adults enter the habitat cell as new individuals.

Two sources of mortality are included in the model. Mortality from predation is explicitly modeled as trophic functional types interact. This includes mortality due to a lack of interaction as well, i.e., when individuals are not able to find food. Also, to maintain reasonable population levels, age-specific background mortality occurs based on a daily mortality rate provided by mortality input parameters.

Design concepts

The design concept metrics detailed below follow those from the standard guidance of reporting individual-based models, including basic principles, emergence, adaptation, objectives, prediction, sensing, interaction, stochasticity, collectives, and observation (Grimm et al. 2006).

The basic principles of the model are those processes that contribute to individual variability and govern trophic interactions. Individual variability is due to both variable life history trait input parameter values and from the unique experiences of individuals

based on spatial discrepancies, differential local resource availability and interactions, and a limited number of stochastic processes. Input data for life history traits can vary across individuals because data values are selected from a triangular distribution of a minimum, mode, and maximum values for each parameter. This is intended to allow for realistic natural variability for traits for which sufficient data exist. Areas where variability is important include pollen production and timing and invertebrate introduction timing. Variability for crop traits is minimized, aside from pollen production, to minimize noise that could potentially overwhelm effects of pests on crop yield and the ability of natural enemies to protect yield.

The objective of individuals is to survive and reproduce. Invertebrates interact with each other and plants, as applicable, during feeding interactions and indirectly through competition for limited food resources. Invertebrate population dynamics and crop yield emerge from individual behavior and the unique interactions of individuals. Certain elements of the model are stochastic including spatial placement of entering invertebrates, direction of dispersal of individuals, and background mortality. Invertebrate individuals can sense their own hunger level, food items within their foraging radius, and herbivores can indirectly sense competition from nearby individuals.

The only “collective” utilized in the model is an aphid colony which is simulated as a single entity, not as individuals. Aphids are modeled as colonies because they are included simply as a food source mass for natural enemies and dynamics of individual

aphids are not a key element of the model. Adaptation of individuals, individual learning, and the ability of individuals to predict is not utilized by the model.

Simulation results are written to a general output file and a matrix that records the amount of material consumed for each trophic functional type combination where feeding occurs. The general output file includes data for each individual for each time step for identity, location, weights of the various compartments that comprise the organism, degree of hunger, and competition level.

Initialization

The model initiates with newly emerged maize plants in the 5 m x 5 m habitat cell. Additional trophic functional types are added at specific times. State variables of initial individuals entering the plot are fixed therefore initialization does not contribute to variability. The complete set of parameter values can be found in Chapter 2.

Input data

The model loads input files that are modified from one set of simulations to the next to represent different scenarios. These files include environmental parameters, individual traits, colonization timing, and timing and effects of managements such as insecticide treatment. Two additional input files are related to trophic interactions including a matrix of functional types specifying food conversion efficiency and one for food preference assignment.

The environmental traits file includes general information about the simulation such as number of simulations, plot size, planting rate, etc., but also some parameters that apply broadly to multiple functional types (e.g., pollen degradation rate). The initial traits file includes values related to the basic natural history of the organism, e.g., when does it enter the plot, how large is it at that time, what does it eat, developmental details, etc. As described above, three values can be added for a parameter representing the minimum, mode, and maximum of values for a given parameter. Input values were obtained from the literature (direct parameterization) or determined by using reasonable values or by trial and error to obtain realistic results (reverse parameterization). No variability was added to a parameter if variable values were not available from the literature or if variability for that parameter was not of key interest. Values were converted to dry weight for plants and invertebrates to simplify modeling the plant.

The food conversion matrix input file is typically populated with values that represent the efficiency with which an organism utilizes the food it ingests for secondary production. In some cases, e.g., ECB, this value is based not on a realistic conversion rate from the literature but is reduced to allow the feeding of ECB to a level of damage that approaches reality. Otherwise, it is difficult to simulate injury to the plant simply based on the large size and robust growth of the maize plant.

The food preference matrix contains values for the probability of feeding interactions between functional types. Adult and immature food preferences are generally the same but can vary depending on the functional type. Adults may maintain the same

feeding preference as the immature stage (e.g., lady beetles) or adults may be assigned to not feed at all (e.g., ECB). The one exception to this includes lacewing adults that differ from the larval diet of aphids, pollen, cannibalism, and intraguild predation by feeding only on pollen. This exception was added as an important distinction of the life history of the green lacewing from lady beetles. Adults moths that do not feed utilize an individual trait input that allows a portion of energy from the pupal stage for use in egg production.

Submodels

Figure 1 provides a flow diagram of the model including the subset of submodel processes used in TrophicLINK. The submodels of TrophicLINK are detailed in Caron-Lormier et al. (2011) and Chapter 2. Submodels utilized for the project include individual emergence, mortality, initial weight, foraging, dispersal, reproduction, growth, development, respiration, maize pollen production, and food preference.

Trophic functional types

The growth and development of the maize plant was modeled based on raw data from Dohleman and Long (2009) of approximately bi-weekly measurements of maize plant weights collected from a field in Illinois (F. Dohleman, personal communication). Physiological maturity of maize plants was on day 120 and at that time whole plant weight was 310 g and grain yield was 144 g dry weight under ideal conditions. Maize pollen production was modeled to vary in a similar way as would be expected in a maize field including a variable start date and span of pollen flow for individual plants.

The result of the parameterization related to pollen was temporally and spatially variable pollen production lasting for14 days overall with each plant shedding pollen from five to eight days (Purseglove 1972). Each plant produced a total of just over 1 g of pollen in total (Porter 1981); however, in the model it degrades by a 20% daily rate to mimic loss of pollen due to environmental factors such as wind and rain. Parameterization of pollen results in initiation of pollen production by a few plants on day 57, peak number of plants producing pollen on day 62, with the last plants producing pollen on day 66. Thus, peak pollen mass occurs on day 65 at approximately 0.4 g of pollen per plant and declines from there rapidly until very little pollen is available by day 80.

The invertebrate functional types were parameterized to mimic patterns of growth and development of the actual insect. Key parameter values and growth and development results for ECB, lady beetle, and lacewing are presented in Table 1. The growth and development results in Table 1 are from simulations run under "non-stress" conditions with abundant food and no predation and so represent best case values for the trophic functional types. Aphid colonies initiate from a single aphid entering the patch from day 41-46, grow to a maximum of 2.5 grams on day after flowering and decline based on a daily senescence rate of 0.12 which initiates when the colony becomes senescent after 43 days. This pattern of growth and decline of aphid colonies was selected to mimic typical aphid colonies in maize fields (Park and Obrycki 2004). Aphids were introduced into the plot at a rate of three aphids/m^2 which resulted in 21% of plants infested with aphid colonies which agrees with Park and Obrycki (2004) who report approximately 20% of

maize with aphids at Iowa field sites. As a result, aphids were sparsely populated in the plots and not immediately available as prey for natural enemies not in close proximity to aphids.

The insecticide application scenario was included to also provide results from a conventional control approach. A single application was implemented on day 65 as a management measure for ECB using the managements input files. Mason et al. (1996) report a 35-72% efficacy of insecticide applications for ECB depending on timing. A 55% control level was used here. The spray was parameterized to cause 50% mortality to natural enemies (Armenta et al. 2003, Dively et al. 2003). Aphid mortality from the application was parameterized to be 70% since by this time in the season the whorl would be open and aphids exposed.

Simulation experiments

Testing, sensitivity analysis, and validation. Sensitivity analyses conducted previously include the following parameters: influence of juvenile mortality on plant weight and yield, herbivore feeding preference, invertebrate foraging radius, daily pollen degradation rate, and dispersal cost (Caron Lormier et al. 2011, Chapter 2). Results of these analyses found the model behaving as expected and consistently.

Simulation scenarios. Scenarios developed were intended to assess for the effect of prey removal on the performance of natural enemies to manage pests (biological control), and maintain or increase their own populations, and protect yield. Scenarios are listed below with abbreviations in parentheses:

1. Maize alone (Maize alone)
2. Conventional maize untreated + pests only, high ECB pressure (Pests only, high ECB)
3. Conventional maize untreated + pests only, lower ECB pressure (Pests only, low ECB)
4. Conventional maize untreated + pests + natural enemies, high ECB pressure (No control, high ECB)
5. Conventional maize untreated + pests + natural enemies, low ECB pressure (No control, low ECB)
6. Conventional maize treated + pests + natural enemies, high ECB pressure (Insecticide, high ECB)
7. Conventional maize treated + pests + natural enemies, low ECB pressure (Insecticide, low ECB)
8. Lepidopteran-resistant Bt maize, shorter term when ECB adult, eggs, and neonate larvae present, high ECB pressure (Bt short, high ECB)
9. Lepidopteran-resistant Bt maize, shorter term when ECB adult, eggs, and neonate larvae present, low ECB pressure (Bt short, low ECB)
10. Bt maize, long term mimicking regional suppression of ECB (Bt long)

The insecticide spray treatment was included based on the importance of being able to position results against chemical insecticide alternatives (Gatehouse et al. 2011). Twenty simulations were run for each scenario to minimize variability (see Chapter 2). The mass of pests and natural enemies, the mass of food items consumed by each invertebrate trophic functional type, and maize yield were evaluated for each scenario. Relative difference across scenarios was assessed using mean values across simulations and 95% confidence intervals.

Results

The total mass of each herbivore trophic functional type plotted over time for each scenario shows reductions in pest populations with the addition of natural enemies

and an insecticide application (Fig. 3.2). Mean peak mass values for aphids was highest in the pests only scenario at 193.1 g, 95% CI [192.7, 193.4] and was reduced by over 70% in the insecticide, ECB high scenario with a mean peak mass of 51.4 g 95% CI [47.7, 55.1] (Table 3.2). The scenarios including natural enemies exhibited reduced mean aphid peak mass by similar amounts with mean aphid peak values ranging from 174.8 – 176.0 g or percent reductions of 8.9 to 9.5% (Table 3.2). Natural enemies are not able to more significantly reduce aphid mass based on the relatively small mass of natural enemies compared to aphid colony mass and poor alignment of temporal overlap conducive to aphid control that often occurs in maize (Foott and Timmins 1973, Elliott et al. 1988).

ECB mass was highest in the pests only, ECB high scenario with a mean peak mass value of 895.5 g, 95% CI [887.2, 903.8] (Table 3.2). Peak ECB mass for the insecticide, high ECB scenario was reduced by over 70% to 247.4 g, 95% CI [241.7,253.1] (Table 3.2). Peak ECB mass for the insecticide, low ECB scenario was likewise reduced by over 70% from 283.1 g in the pests only, ECB high scenario to 76.7 g, 95% CI [74.0,79.4] (Table 3.2). ECB mass does not vary in Fig. 1 for the Bt short and Bt long scenarios because ECB was controlled by Bt maize in those scenarios with only ECB eggs and early larvae being present or no ECB present at all for the Bt short and Bt long scenarios, respectively. The no control scenarios had a mean ECB peak mass of 635.3 g, 95% CI [622.5, 648.1] for the ECB high scenario and a mean peak mass of 196.8 g, 95% CI [622.5, 648.1] for the ECB low scenario, demonstrating that the natural enemies partially reduced the ECB population by 29.1% and 30.5%, respectively. ECB

population reduction by natural enemies occurred through feeding on eggs and larvae for the brief time they were available before larvae bored into the plant. The amount of maize plant consumed by aphids and ECB is consistent with the mass of pests across the season curves and peak mean mass showing reductions in the amount of plant consumed as herbivore populations were reduced by either natural enemies or insecticide (Fig. B.1). Maize yield across scenarios is presented in Table B.1 demonstrate yield reductions due to the varying pest populations and partial yield protection with Bt maize and insecticide management measures.

The mass of natural enemies plotted over time shows similar curves for the lady beetle and lacewing trophic functional types across scenarios except for the insecticide scenario that reduced the mean peak population mass by 65.2 and 77.8%, respectively (Fig. 3.2). Mean peak mass for lady beetle was 2.3 g 95% CI [2.1, 2.4], 2.0 g 95% CI [1.9, 2.2], 2.1 g 95% CI [1.9, 2.3], 2.1 g 95% CI [2.0, 2.3], and 2.1 g 95% CI [1.8, 2.3] for the no control, high ECB; no control, low ECB; Bt short, high ECB; Bt short, low ECB, and Bt long scenarios, respectively (Table 3.2). Peak mass for the lacewing trophic functional type was 1.8 g 95% CI [1.6, 2.1], 1.8 g 95% CI [1.6, 2.0], 1.7 g 95% CI [1.5, 2.0], 1.8 g 95% CI [1.6, 2.0], 1.7 g 95% CI [1.5, 1.8] for the no control, high ECB; no control, low ECB; Bt short, high ECB; Bt short, low ECB, and Bt long scenarios, respectively (Table 3.2). The amount of different food types consumed by natural enemies is presented in the Figs B.2 and B.3.

Discussion

Natural enemies were exposed to scenarios with reduced prey options due to Bt maize control of ECB. Prey reduction was at two levels based on a Bt maize short-term scenario where ECB adults were present and ECB eggs and early larvae were available as prey for natural enemies. The second level of prey reduction was represented by the Bt maize long-term scenario mimicking regional suppression of ECB resulting in an absence of any ECB life stage for natural enemy prey. ECB prey availability also varied based on two infestation levels of ECB. Growth and development of the lady beetle and lacewing natural enemy trophic functional types was overall similar across scenarios indicating that they were able to successfully utilize the other available food resources, maize pollen and aphids, in the absence of ECB prey. The insecticide caused considerable reduction of each trophic functional type.

The highly disturbed nature of annual agricultural systems inherently limits the biodiversity of agricultural fields. Generalist natural enemies like lady beetles and lacewings are well-adapted to this habitat due to their ability to be highly vagile, polyphagous, effective at searching for prey, highly competitive, and to have high reproductive capacities (Wiedenmann and Smith 1997). Though field studies evaluating Bt crops have not reported consistent effects on natural enemies, lab studies evaluating for prey-mediated effects have found natural enemies sensitive to prey quality. Clearly, the ability of natural enemies to utilize alternative prey and non-prey food resources is

key for their persistence in agricultural fields (Musser and Shelton 2003a, Lundgren 2009b, Choate and Lundgren 2013, Schmidt et al. 2013, Wong and Frank 2013).

The lady beetle trophic functional type, modeled generally on *C. maculata*, had a high affinity for maize pollen. Maize pollen is reported as a preferred food for *C. maculata* in nature and they can complete development in maize pollen only (Smith 1960, Lundgren et al. 2005b). This natural enemy would be expected to be resilient to the effect of a relatively minor prey resource such as ECB eggs and small larvae. The results of these simulations support this. The need for *C. maculata* to rely heavily on maize pollen alone, though, may result in increased risk of mortality because larval developmental times on pollen are considerably longer compared to development when feeding on aphids (Lundgren and Wiedenmann 2004) and maize pollen availability is highly uncertain depending on timing and abiotic conditions.

The lacewing trophic functional type had a low affinity for maize pollen reflecting the inability of functional type modeled on *C. carnea* to develop through the larval stage when feeding on maize pollen only (Meissle et al. 2014). Maize pollen can be a key element in the diet of the *C. carnea*, allowing it to persist through time of low availability of preferred food (Meissle et al. 2014). The lack of the ability of *C. carnea* to completely rely on pollen for development explains why mean peak mass of the lacewing trophic functional type was reduced by 13% more than the mean peak mass of the lady beetle in the same scenario. The lack of strong affinity for pollen may also account for the

lacewing mean peak mass being the lowest in the Bt long scenario though confidence intervals overlapped with the other non-insecticide scenarios.

This analysis was intended to be a first step exploring the opportunity afforded by Bt maize where certain insect pests are removed while conserving beneficial insects. To achieve this, a simplified system was evaluated to step back from the complexity of the field and focus in on the result of plant-pest-natural enemy interactions that would potentially result in effects from reduced prey availability. The simplified system also offered the chance to continue to pressure test the TrophicLINK model. The situation evaluated here included lepidopteran-resistant Bt maize, a single susceptible lepidopteran pest, a non-susceptible aphid, and two generalist predators, a lady beetle and a lacewing. Investigation into more complicated scenarios that already exist in the field, including Bt maize that controls additional insect pests, and addition of more field level complexity including higher diversity of predators and prey is worth exploring. For example, Schuler et al. (2005) did detect a negative effect on a natural enemy related to prey reduction as they dropped the level of abundance of the non-susceptible prey in their cage study of Bt oilseed rape. So, not surprisingly, the limit exists. Based on these simulation results, however, the adaptability of generalist predators allows them to maintain similar population levels despite a reduction in ECB prey due to Bt maize.

Acknowledgments

The authors would like to acknowledge the following contributions to this project: F. Dohleman for providing maize plant growth measurement data; A. Martin and J.

Uffman of Monsanto Company for rearing European corn borer and other insects to generate measurements used to support parameterization; G. Caron-Lormier for his support in understanding of TrophicLink and making initial modifications to the model, and, lastly, a debt of gratitude is owed to scientists that have contributed to the extensive body of literature relied on to parameterize the model.

Table 3.1. Key parameter values and growth and development outcomes under ideal conditions for the ECB, lady beetle, and lacewing trophic functional types[1]

Characteristic	ECB	Lady beetle	Lacewing
Initial abundance (per m^2)	3 per m^2	0.5 per m^2	0.5 per m^2
Entrance day[2]	58; 60, 64, 68	60; 60, 63, 66	60; 60, 63, 66
Max initial egg load (# eggs/5x5 m patch)[3]	High: 6800 Low: 2170	845	740
Single egg weight (g)	0.00001	0.000052	0.000022
Time to egg hatch (days)	4	4	5
Larval development time (days)[4]	16	12	12
Foraging radius (m)	0.5	0.3	0.3
Pupal stage (days)[5]	n/a	7	15
Maximum weight of larva (g) [4]	0.119	0.012	0.09
Peak population mass (g)[6]	High: 895.5 (17.7) Low: 283.1 (8.5)	5.4 (0.2)	4.5 (0.4)

[1] Key aspects of the remaining trophic functional type, aphids, are described in the methods because aphids are not modeled as individuals. Max initial egg load, larval development time, and peak mass represent "Ideal conditions", i.e., abundance of a preferred food type and no predation.

[2] The first number is entered in the colonization input file and the second set represents the minimum, mode, and maximum values of the initial abundance parameters from the initial traits input file.

[3] Total eggs deposited by initial adults

[4] Larval development time and maximum weight outcomes are the result of the combined parameter values of developmental constant, food demand, and energy to growth. The larval development is delayed when individuals are not able to acquire sufficient food.

[5] ECB were assumed to overwinter as pupae so second generation adults were not included in the simulation.

[6] Mean (SE)

Table 3.2. Mean peak mass of the herbivore and natural enemy trophic functional types from each scenario[1]

Invert Functional Type	Scenario								
	Pests only, ECB high	Pests only, ECB low	No control, ECB high	No control, ECB low	Bt short, ECB high	Bt short, ECB low	Bt long	Insecticide, ECB high	Insecticide, ECB low
Aphid	193.1 g (192.7, 193.4)	193.1 g (192.8, 193.4)	175.4 g (173.6, 177.2)	176.0 g (174.2, 177.7)	174.8 g (172.8, 176.7)	175.8 g (174.0, 177.6)	176.03 g (174.6, 177.5)	51.4 g (47.7, 55.1)	55.2 g (49.5, 60.9)
ECB	895.5 g (887.2, 903.8)	283.1 g (279.2, 287.1)	635.3 g (622.5, 648.1)	196.8 g (194.1, 199.5)	< 1g	< 1g	N/A	247.4 g (241.7, 253.1)	76.69 g (74.0, 79.4)
Lady beetle	N/A	N/A	2.3 g (2.1, 2.4)	2.0 g (1.9, 2.2)	2.1 g (1.9, 2.3)	2.1 g (2.0, 2.3)	2.1 g (1.8, 2.3)	0.8 g (0.7, 0.9)	0.9 g (0.8, 1.0)
Lacewing	N/A	N/A	1.8 g (1.6, 2.1)	1.8 g (1.6, 2.0)	1.7 g (1.5, 2.0)	1.8 g (1.6, 2.0)	1.7 g (1.5, 1.8)	0.4 g (0.3, 0.5)	0.5 g (0.4, 0.6)

[1]Mean number (95% CI upper limit, 95% CI lower limit)

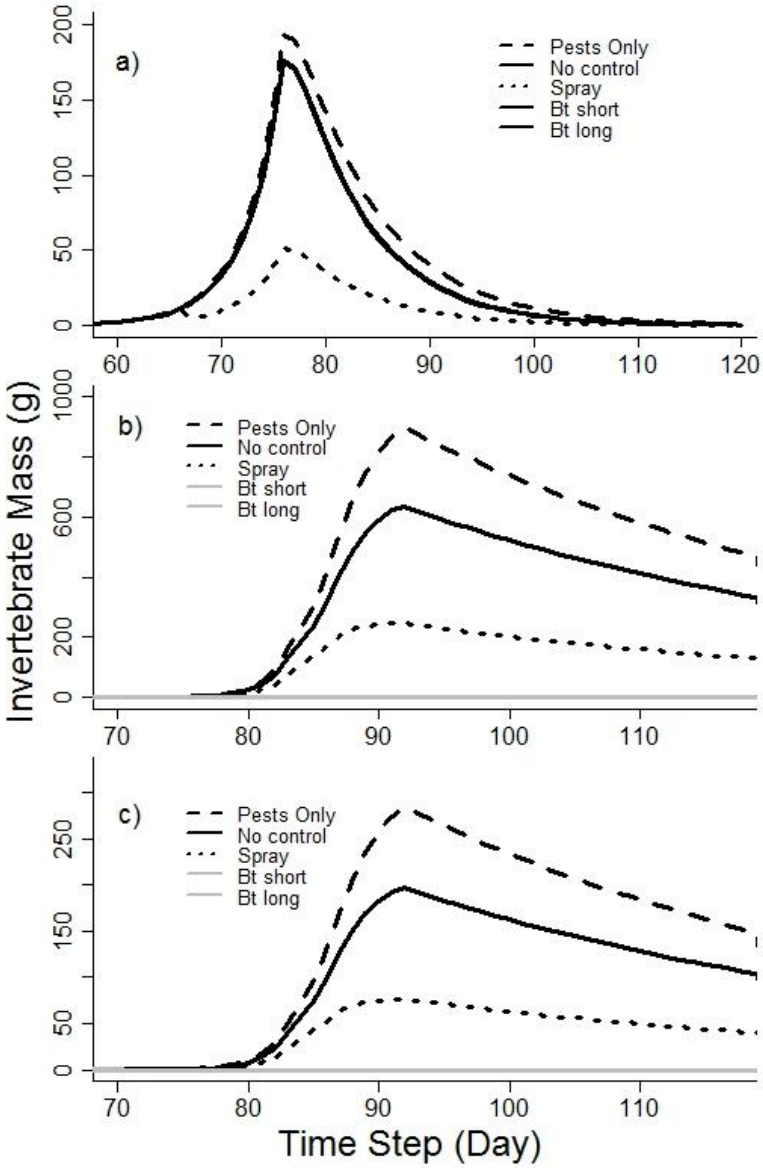

Figure 3.1. Herbivore trophic functional type mass across the season for each scenario for a) aphid, b) European corn borer with high infestation, and c) European corn borer with low infestation. Scenarios included pests only and others with natural enemies including no control measures, insecticide spray, Bt short term planting, and Bt long with regional suppression of ECB. For aphids, the No control, Bt short, and Bt long lines overlap forming single line. For ECB, the Bt short and Bt long scenarios have either only initial eggs and larvae or no ECB at all, respectively, resulting in flat lines.

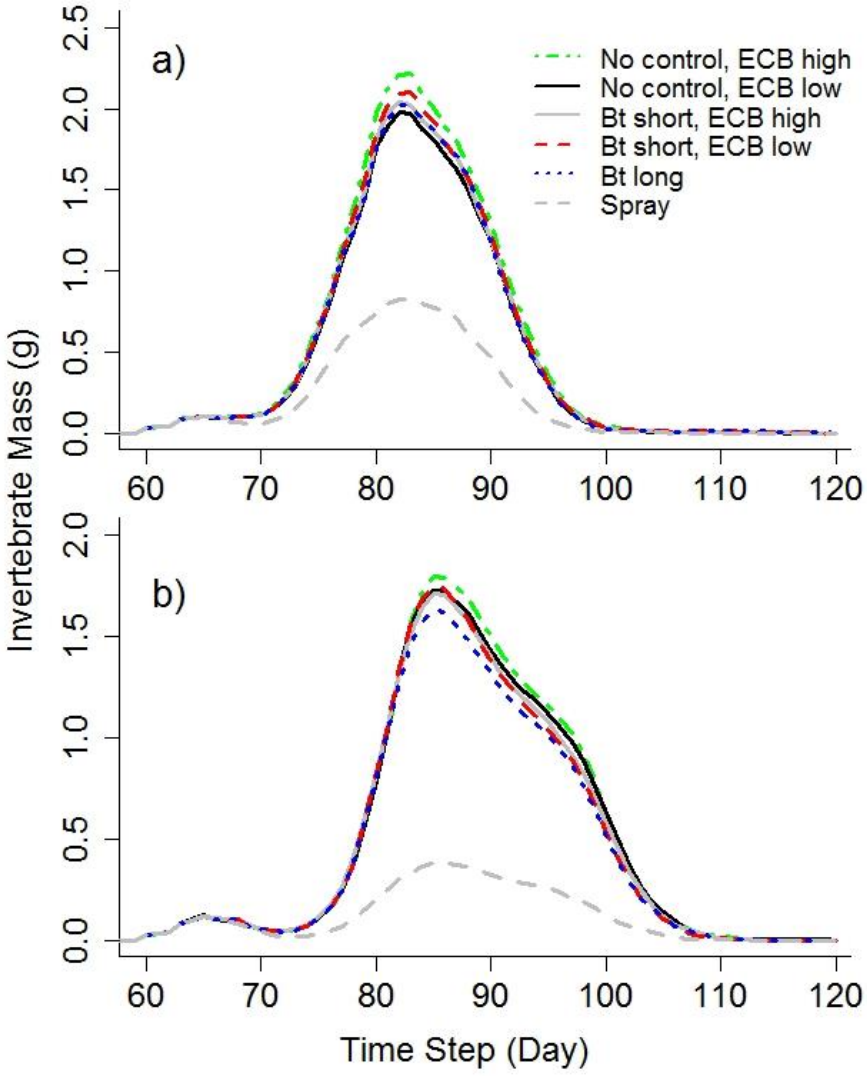

Figure 3.2. Natural enemy trophic functional type mass across the season for each scenario for a) lady beetle and b) lacewing. Scenarios included no control measures with high ECB infestation, no control measures with low ECB measures, Bt short term planting (includes ECB eggs and early larvae), Bt long term planting (no ECB present), and insecticide spray.

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APPENDICES

APPENDIX A

CHAPTER 2 SUPPORTING INFORMATION

Table A.1. Initial traits input file parameter descriptions

Parameter	Functional Type	Description
Background mortality	All	Juvenile, adult and senescent stages of organisms are assigned daily "background" mortality rates. Mortality otherwise occurs in the model due to predation and stresses such as lack of food.
Developmental stage at adult	All	Upon becoming adults, organisms are assigned a value of 1. Invertebrates progress through the immature stage with values ranging from > 0 to less than 1. Plants are considered either seeds or adults.
Switch to senescent	All	Age when a trophic functional type becomes senescent. Senescent mortality is applied at this time.
First emergence	All	Time step when a trophic functional type enters the simulation.
Egg incubation	Invertebrates	Number of days for eggs to hatch.
Initial weights	All	Initials weights are assigned to individuals entering the simulation including values for initial base weight, free store weight, propagule weight.
Energy producing ratio	Plants	Proportion of plant that contributes to energy production.
Relative growth rate	Plants	Applies to plant growth.
Foraging radius	Invertebrates	Delimits the area where an individual checks neighbors for potential trophic interactions.
Dispersal distance	Invertebrates	Distance an adult and immature invertebrate can travel when prompted by starvation or competition.
Cost of dispersal	Invertebrates	Energy cost of dispersing.
Herbivore overcrowding	Plants	Value assigned to plants representing the tolerance of plants to herbivores. Values range from 0 to 1 with values approaching 1 causing herbivores to disperse from the overpopulated plants.
Weight of a single propagule	All	Used to determine number propagules that will be created from the weight of existing weight available to produce propagules.
Switch to reproductive age	Plants	Days until plants begin shunting energy towards reproduction.
Reproductive ratio	All	Threshold for seed shattering for plants and oviposition for invertebrates based on percent of energy accumulated in propagule compartment.
Ratio free store to base	All	Ratio of base weight to free store weight for plants. Energy allocated to growth for invertebrates.
Free store to propagule	All	Energy allocated to propagule production.
Max weight	Plants	Maximum vegetative mass (i.e., base weight) of plant.
Free store to pollen	Plants	Energy allocated to pollen production.
Time as pupae	Invertebrates	Time in days that an invertebrate remains in the pupal stage.
Total weight after pupal stage (%)	Invertebrates	Percent weight reduction of adults relative to initial weight of pupa.

Table A.1. (continued). Initial traits input file parameter descriptions

Parameter	Functional Type	Description
Pollen duration	Plants	Length of time in days of pollen release.
Pollen start	Plants	Age of plant when pollen release initiates.
Free store to adult	Invertebrates	Relevant only to adults that do not feed in the model (e.g., moth adults). This percentage of weight of pupae that is transferred to the adult stage as propagule weight. Non-feeding adults need a value for max eggs to prevent them from ovipositing their complete propagule weight on the first day.
Max eggs	Invertebrates	Maximum number of eggs an adult can oviposit per day. Relevant to adults that do not feed and have a freestore to adult value. This prevents adults from ovipositing their entire propagule weight on a single day.
Initial abundance	All	Represents the initial abundance of individuals per square meter. Individuals can also enter the plot using the colonization matrix.
Food demand	Invertebrates	Daily food requirement of an individual.
Respiration cost	Invertebrates	Cost of respiration expressed as a percent of an individual's weight.
Biotype	All	Associates individuals with a particular functional type. Plant = 1, invertebrates = 2.
Developmental constant	Invertebrates	Represents growth rate and determines the amount of time an immature invertebrate requires to reach pupation.
Age of entering individual	All	Age of an individual entering the plot.
Development state of entering individual	All	Developmental state of an individual entering the plot.
Plant part fed upon by immature	Invertebrates	Immature invertebrate can specifically feed on seeds (i.e. grain), leaf, free store (i.e., phloem), base weight, or pollen.
Plant part fed upon by adult	Invertebrates	Invertebrate adults can specifically feed on seeds (i.e. grain), leaf, free store (i.e., phloem), base weight, or pollen.

Table A.2. Maize trait parameter values[1]

Parameter	Value	Supporting information
Background mortality	0	Sensible value and minimized variability within the crop
Developmental stage at adult	1	Model specific value designates plant from a seed
First emergence (day)	1	The season starts with seedling emergence on day 1
Initial weight	1 g	Sensible value
Energy producing ratio	0.5	Sensible value
Relative growth rate	0.16	Leroux and Long (1994)
Tolerance of neighbors	0.1	Caron-Lormier et al. (2009)
Weight of a single propagule	250 mg	Leakey et al. (2006)
Switch to reproductive age	64 days	Approximate timing of initiation the reproductive stage in maize
Reproductive ratio	1	Sensible value. Set high to prevent maize from dropping seeds
Ratio free store to base	0.1	Caron-Lormier et al. (2009)
Free store to propagule	0.32	Caron-Lormier et al. (2009)
Free store to pollen[2]	0.035	Reverse parameterization to enable plant to produce realistic amount of pollen (Porter 1981, Nowakowski and Morse 1982).
Max weight	155 g	Vegetative mass, Dohleman and Long (2009)
Pollen duration	5, 6.5, 8 days	Purseglove (1972)
Pollen start	57, 62, 66	Approximate timing of initiation of maize anthesis
Initial abundance	14 m^2	Typical maize planting density
Biotype	1	Model specific value, Plant = 1
Age of entering individual	1 day	Newly emerged plant
Development state of entering individual	1	Model specific value

[1] Multiple parameter values represent the minimum, mode, and maximum values.
[2] Calculations for pollen production per plant: 5 million grains produced per plant * pollen grain weight of $247x10^{-9}$ = 1.24 g of pollen.

Table A.3. Aphid "super" individual trophic functional type individual trait parameter values[1]

Parameter	Value	Notes, supporting information
Background mortality	0.1	Colony growth is based on individual aphid growth including background mortality. The senescent mortality value (0.1) is used as a daily colony degradation rate once it becomes senescent.
Developmental stage at adult	1	Designated as adult but aphids are unique in that they both grow and reproduce concurrently
Switch to senescent	43 days	Park and Obrycki (2004), Foott (1977)
First emergence (day)	40, 43, 46	Park and Obrycki (2004)
Egg incubation	0	Not applicable, simulated aphids produce live young
Initial weights	0.00018	Base:0.00011, free: 0.000025, Prop: 0.000042
Foraging radius	0.5 m	Sensible value
Dispersal distance	N/A	Aphid colonies do not disperse
Cost of dispersal	N/A	Aphid colonies do not disperse
Weight of a single propagule	0.00001 g	Gao et al. (2010)
Reproductive ratio	0.12 g	Sensible value
Development stage at adult	1	Model specific value
Ratio free store to base	0.45	Reverse parameterization to match individual aphid trophic functional type
Free store to propagule	0.3	Reverse parameterization to match individual aphid trophic functional type
Time as pupae	0	Not applicable, no pupal stage for Hemiptera
Total weight after pupal stage	0	Not applicable, no pupal stage for Hemiptera
Free store to adult	N/A	Only applies to adults that do not feed
Initial abundance	3 m^2	Results in ~20% of plants infested as reported by Park and Obrycki (2004)
Food demand	0.5	Reverse parameterization, balance with free store to propagule
Respiration cost	0.028	Caron-Lormier et al. (2009)
Biotype	2	Identifies the functional type as an invertebrate.
Developmental constant	0.004	Reverse parameterization to match individual aphid trophic functional type
Age of entering individual	10 days	Sensible value
Development state of entering individual	1	Entering super aphids are classified as adults
Plant part fed upon by immature	2	Identifies the part of the plant fed upon, i.e., freestore energy/sap for aphids
Plant part fed upon by adult	2	Identifies the part of the plant fed upon, i.e., freestore energy/sap for aphids

[1] Multiple parameter values represent minimum, mode, and maximum values.

Table A.4. European corn borer trophic functional type trait parameter values[1]

Parameter	Value	Notes, supporting information
Background mortality (juvenile)	0.01	Showers et al. (1989)
Background mortality (adult)	0.009	Raybould et al. (2011), model assumption
Background mortality (senescent)	0.6	Reasonable value to cause mortality of senescent individuals
Developmental stage at adult	1	Model specific value to differentiate immature from adult
Switch to senescent	N/A	ECB do not become senescent since this is modeled as an overwintering generation
First emergence (day)	59, 64, 69	Mason et al. (1996)
Egg incubation	4 days	Mason et al. (1996)
Initial base weight	0.01026	Collective initial weight is 17 mg (Table C.3.). Apportioned rates based on Caron-Lormier (2009).
Initial freestore weight	0.0057	Collective initial weight is 17 mg (Table C.3.). Apportioned rates based on Caron-Lormier (2009).
Initial propagule weight	0.00114	Collective initial weight is 17 mg (Table C.3.). Model assumption that resulted in reasonable oviposition by adults.
Maximum oviposition/day	16	Specific to adults that do not feed. Prevents oviposition of all eggs at once.
Foraging radius	0.5 m	Sensible value
Dispersal distance	3 m	Sensible value
Cost of dispersal	0.001	Caron-Lormier (2009)
Weight of a single propagule	0.000015 g	Measurement made for this project, see Table C.3. Weights were converted to dry weight.
Reproductive ratio	0.12	Sensible value based on reverse parameterization.
Ratio free store to base	0.9	Results in reasonably sized adult in coordination with developmental constant and food demand. Based on Caron-Lormier et al. (2009).
Free store to propagule	0.2	Results in reasonably sized adult in coordination with developmental constant and food demand. Based on Caron-Lormier et al. (2009).
Time as pupae	100 days	Modeled as overwintering generation
Total weight after pupal stage	0.25	Lab data generated for this project
Free store to adult	0.65	Carryover of energy from immature stage to adults enables adult survival
Initial abundance	3 m^2	Sensible value, reverse parameterization to obtain appropriate initial egg loads
Food demand	0.75	Reverse parameterization to obtain larval weight of ~20 mg (Table C.3.)
Respiration cost	0.028	Caron-Lormier et al. (2009)
Biotype	2	Identifies the functional type as an invertebrate
Developmental constant	0.0043	Reverse parameterization to obtain larval development period of 16 days (Table C.3.)
Age of entering individual	15	Sensible value
Development state of entering indiv.	1	Adults ECB enter the patch
Plant part fed upon by immature	0	Indicates all plant compartments except pollen are fed upon
Plant part fed upon by adult	99	Indicates adults that do not feed

[1] Multiple parameter values represent minimum, mode, and maximum values.

Table A.5. Lady beetle trophic functional type trait parameter values[1]

Parameter	Value	Notes, supporting information
Background mortality (juvenile)	0.01	Dixon (2000)
Background mortality (adult)	0.01	Raybould et al. (2011), model assumption
Background mortality (senescent)	0.4	Reasonable value to cause mortality of senescent individuals
Developmental stage at adult	1	Model specific value to differentiate immature from adult
Switch to senescent (age in days)	22 days	Reasonable longevity for lady beetle under field conditions.
First emergence (day)	60; 60, 63, 66	Timing corresponds to maize anthesis when arthropods are most actively colonizing the crop.
Egg incubation	4 days	Phoofolo and Obrycki (1997), Table C.7.
Initial base weight	0.0025	Collective initial weight is 5 mg (Lundgren and Wiedenmann 2005). Apportioned rates based on (Caron-Lormier et al. 2009).
Initial freestore weight	0.0016	Collective initial weight is 5 mg (Lundgren and Wiedenmann 2005). Apportioned rates based on Caron-Lormier (2009).
Initial propagule weight	0.001	Collective initial weight is 5 mg (Lundgren and Wiedenmann 2005). Model assumption that resulted in reasonable oviposition by adults.
Foraging radius	0.3	Sensible value
Dispersal distance (immature)	2 m	Sensible value
Dispersal distance (adult)	3 m	Sensible value given plot size of 5 x 5 m. Note that individuals cannot emigrate beyond the patch.
Cost of dispersal	0.001	Sensible value based on reverse parameterization. Simulation assumption from Caron-Lormier et al. (2009).
Reproductive ratio	0.05	Sensible value based on reverse parameterization.
Weight of a single propagule	0.000052 g	Measurement made for this project, see Table C.7. Weights were converted to dry weight.
Ratio free store to base	0.75	Results in reasonably sized adult in coordination with developmental constant and food demand. Based on Caron-Lormier et al. (2009).
Free store to propagule	0.11	Based on Caron-Lormier et al. (2009).
Time as pupae	7 days	Phoofolo and Obrycki 1997
Total weight after pupal stage	0.72	Lundgren and Wiedenmann (2005), Santos-Cividanes et al. (2010)
Free store to adult	N/A	Applies to non-feeding adults
Initial abundance	0.5 m^2	Sensible value
Food demand	0.62	Reverse parameterization to obtain larval weight of 9 mg (Santos-Cividanes et al. 2010)
Respiration cost	0.027	Caron-Lormier et al. (2009)
Biotype	2	Identifies the functional type as an invertebrate.
Developmental constant	0.0052	Reverse parameterization to obtain larval development period of 12 days (Santos-Cividanes et al. 2011)
Age of entering individual	17 days	Sensible value
Development state of entering indiv.	1	Adult lady beetles enter the patch
Plant part fed upon by immature	4	Identifies plant compartment fed upon: pollen = 4
Plant part fed upon by adult	4	Identifies plant compartment fed upon: pollen = 4

[1] Multiple parameter values represent the minimum, mode, and maximum values.

Table A.6. Lacewing trophic functional type trait parameter values[1]

Parameter	Value	Notes, supporting information
Background mortality (juvenile)	0.01	Dixon and Dixon (2000)
Background mortality (adult)	0.01	Raybould et al. (2011), model assumption
Background mortality (senescent)	0.4	Reasonable value to cause mortality of senescent individuals
Developmental stage at adult	1	Model specific value to differentiate immature from adult
Switch to senescent (age in days)	17	Reasonable longevity for lady beetle under field conditions (Osman and Selman 1996, Colares et al. 2015).
First emergence (day)	60; 60, 63, 66	Timing corresponds to maize anthesis when arthropod abundance increases in maize.
Egg incubation	5 days	Venzon et al. (2006)
Initial base weight	0.0023 g	Collective initial weight is approx. 3 mg (Zheng et al. 1993). Apportioned rates based on Caron-Lormier (2009)
Initial freestore weight	0.0003 g	Collective initial weight is approx. 3 mg (Zheng et al. 1993). Apportioned rates based on Caron-Lormier (2009).
Initial propagule weight	0.00022 g	Model assumption that resulted in reasonable oviposition by entering adults.
Foraging radius	0.3 m	Sensible value
Dispersal distance (immature)	2 m	Sensible value
Dispersal distance (adult)	3 m	Sensible value given plot size of 5 x 5 m. Note that individuals cannot emigrate beyond the patch.
Cost of dispersal	0.001	Sensible value based on reverse parameterization. Simulation assumption from Caron-Lormier et al. (2009).
Weight of a single propagule	0.000022 g	Raybould et al. (2011)
Reproductive ratio	0.05	Sensible value based on reverse parameterization.
Ratio free store to base	0.7	Results in reasonably sized adult in coordination with developmental constant and food demand. Based on Caron-Lormier et al. (2009).
Free store to propagule	0.08	Based on Caron-Lormier et al. (2009).
Time as pupae	15 days	Obrycki et al. (1989)
Total weight after pupal stage	0.7	Zheng et al. (1993), Gao et al. (2007)
Free store to adult	N/A	Applies to non-feeding adults only
Initial abundance	0.5 m^2	Sensible value
Food demand	0.76	Reverse parameterization to obtain larval weight of 8 mg (Obrycki et al 1989).
Respiration cost	0.027	Caron-Lormier et al. 2009
Biotype	2	Identifies the functional type as an invertebrate.
Developmental constant	0.006	Reverse parameterization to obtain larval development period of 12 days (Obrycki et al. 1989)
Age of entering individual	12 days	Sensible value
Development state of entering indiv.	1	Adult lacewings enter the patch
Plant part fed upon by immature	4	Identifies plant compartment fed upon: pollen = 4
Plant part fed upon by adult	4	Identifies plant compartment fed upon: pollen = 4

[1] Multiple parameter values represent the minimum, mode, and maximum values.

Table A.7. Invertebrate efficiency of conversion of ingested food rates when feeding for the different trophic functional type feeding combinations

Feeding Invertebrate	**Food Item**				
	Maize	**ECB**	**Aphid**	**Lady beetle**	**Lacewing**
Aphid	0.15[2]	n/a	n/a	n/a	n/a
ECB	0.05[1]	n/a	n/a	n/a	n/a
Lady beetle	0.15[3]	0.2[4]	0.2[5]	0.2[4]	0.2[4]
Lacewing	0.15[4]	0.3[4]	0.3[6]	0.3[4]	0.3[4]

n/a indicates that no feeding interaction occurs for that trophic functional type combination

[1] Based on inverse parameterization. In the case of ECB feeding on maize, a lower than published conversion rate was used to enable appropriate levels of damage to the plant. A published efficiency of conversion of ingested food for ECB is 0.1 (Houseman et al. 1992)

[2] Add reference for aphid ECI

[3] Actual value as estimated reported by Lundgren and Wiedenmann (2004) is 0.07.

[4] Value selected based on reasonable assumption, typically based on ECI values reported for other types of food.

[5] Value as reported by Isikber and Copland (2001) is 0.22.

[6] Values reported by Zheng et al. (1993) varied from depending species and life stage.

Table A.8. Food preference tier values for the different trophic functional type feeding combinations[1]

Feeding Invertebrate	**Food Item**				
	Maize[2]	**ECB**	**Aphid**	**Lady beetle**	**Lacewing**
Aphid	1	n/a	n/a	n/a	n/a
ECB	1	n/a	n/a	n/a	n/a
Lady beetle	1	2	1	3	3
Lacewing	3	2	1	3	3

n/a indicates that no feeding interaction occurs for that trophic functional type combination

[1] The significance of food preference tier values are as follows: 1 = the feeding invertebrate will always feed on this food type; 2 = the feeding invertebrate will feed on the food item 30% of the time regardless of hunger level and up to 100% of the time as hunger level increases; 3 = the feeding invertebrate will feed on the food item 2% of the time regardless of hunger level and up to 100% of the time as hunger level increases.

[2] Aphids feed on the sap plant compartment, ECB feeds on all plant compartments (except pollen), and lady beetles and lacewings feed on pollen.

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APPENDIX B

CHAPTER 3 SUPPORTING INFORMATION

Table B.1. Maize yield across scenarios

Treatment	Yield[1]
Maize only	144.4 g (144.4, 144.4)
Pests only, ECB high	114.4 g (114.0, 114.8)
Pests only, ECB low	133.8 g (133.6, 134.0)
No control, ECB high	122.9 g (122.3, 123.5)
No control, ECB low	136.6 g (136.5, 136.7)
Bt short, ECB high	142.6 g (142.6, 142.6)
Bt short, ECB low	142.6 g (142.6, 142.6)
Bt long	142.6 g (142.5, 142.6)
Insecticide, ECB high	136.1 g (135.9, 136.4)
Insecticide, ECB low	141.4 g (141.2, 141.6)

[1]Mean number (95% CI lower limit, 95% CI upper limit)

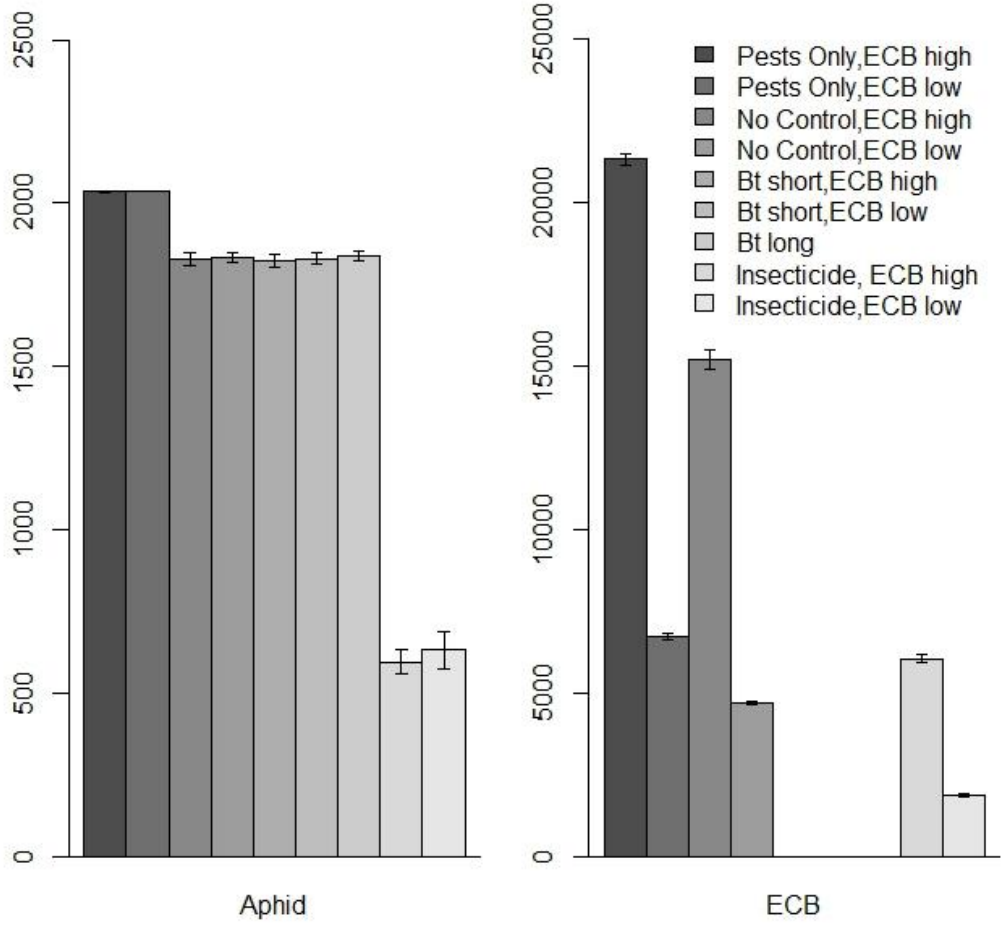

Figure B.1. Amount of plant consumed by the aphid (left) and European corn borer (right) trophic functional type. Error bars are absent from the pests only scenarios for aphids since negligible variability exists for aphid plant consumption under ideal conditions. The gap in the ECB figure results from an absence of ECB in the Bt long scenario and only a negligible amount in the Bt short scenarios.

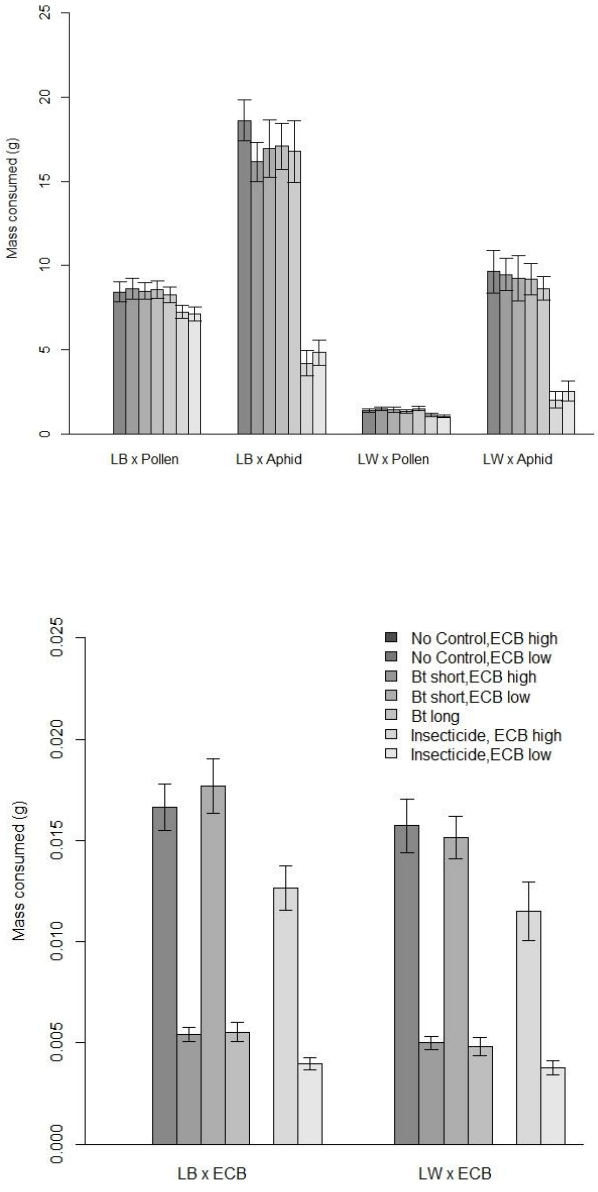

Figure B.2. Amount of pollen and aphid (top) and ECB (bottom) consumed by the natural enemy trophic functional types. Feeding interactions are labeled on the x axis as "feeder x consumed". LB= lady beetle, LW= lacewing. Gaps in the columns are due to the absence of ECB from the Bt long scenario.

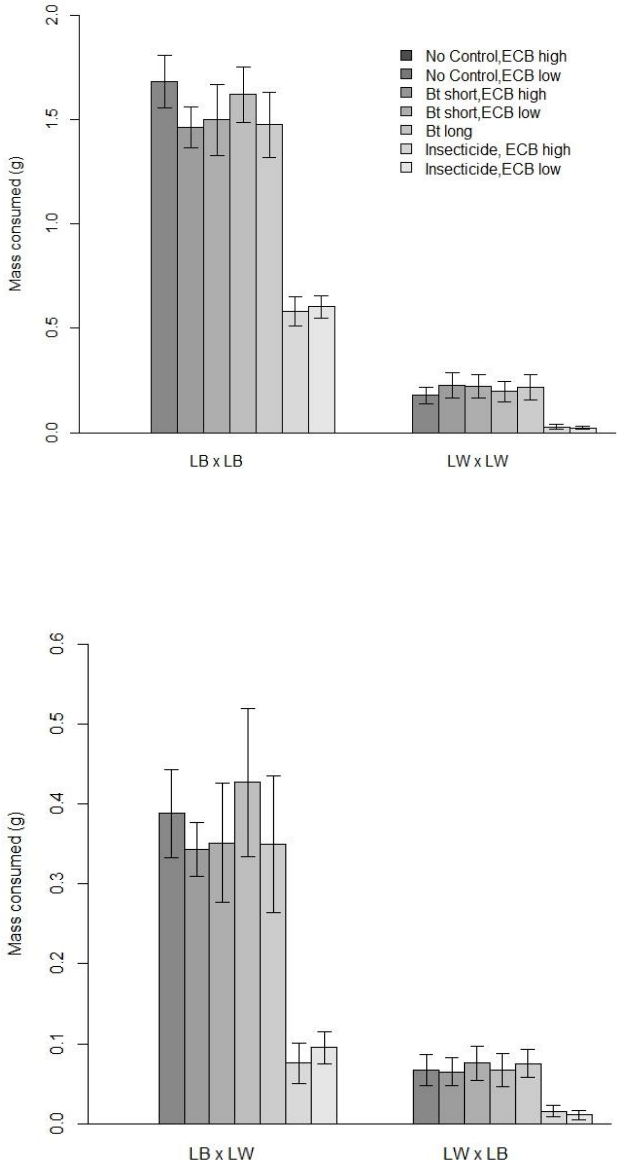

Figure B.3. Amount of food consumption through cannibalism and intraguild predation within the natural enemy trophic functional types. Feeding interactions are labeled on the x axis as "feeder x consumed". LB= lady beetle, LW= lacewing**.**

APPENDIX C

ADDITIONAL INFORMATION GATHERED IN SUPPORT OF THE PROJECT

Copious amounts of information were gathered in support of code modifications as well as model parameterization including some measurements made specifically for the project. A portion of this information is provided here. The initial traits input key table (C.1.) expands on the initial traits table in Appendix A by including all parameters (not only those relevant to the simulations run for this project) as well as the identifiers that correspond to numeric codes contained in the initial traits csv input file.

List of Additional Supporting Information:

Table C.1. Initial traits input file key

Table C.2. Complete list of modifications made to TrophicLink to enable current project

Table C.3. Life history measurements of European corn borer, *Ostrinia nubilalis*, reared at 25 ºC

Table C.4. Developmental measurements of European corn borer, *Ostrinia nubilalis*, reared at 25 ºC

Table C.5. Life history measurements of fall armyworm, *Spodoptera frugiperda*, reared at 25 ºC

Table C.6. Developmental measurements of fall armyworm, *Spodoptera frugiperda*, reared at 25 ºC

Table C.7. Life history measurements of four species of lady beetles (Coleoptera: Coccinellidae)

Table C.1. Initial traits input file key

Trait name Trait # - Parameter #	Parameter Description	Notes
Mortality 0-0	juvenile mortality	Daily mortality rate for juveniles. For examples, 85% of aphids would survive over a 10-day developmental period with a 0.0138 daily mortality rate. Included as 0 for crop plants for these simulations.
Mortality 0-1	adult mortality	Daily mortality rate for adults. Included as 0 for crop plants for these simulations.
Mortality 0-2	senescent mortality	Daily mortality of individuals that become senescent, i.e., individuals that have "switched to senescent" according to the value for parameter Mortality 0-4.
Mortality 0-3	development stage at adult	Upon becoming adults, organisms are assigned a value of 1. Once a seed becomes a plant, it is considered an adult. Growth parameter 7-1 governs when plants become mature, i.e., begin to develop seeds. Invertebrates progress through the immature stage with values ranging from > 0 to less than 1. The value of "1" represents adult invertebrates since Developmental Rate= BaseWeight/MaxBaseWeight. Once the base weight reaches the maximum base weight, the development rates reaches 1. At this point, energy is used for propagule development in invertebrates.
Mortality 0-4	switch to senescent	Age when a trophic functional type becomes senescent. Senescent mortality is applied at this time. Corresponds to senescent mortality (Mortality, 0-2)
Emergence 1-0	first emergence	Number of days after beginning of simulation. could be day 1 if starting within a year or could also be counting from January 1.
Emergence 1-1	second emergence (plants); egg incubation time (inverts)	For plants, represents second flush of weeds or next round of crop. For invertebrates, days for egg incubation.
Weight 2-0	initial base weight	Relevant to individuals entering a simulation. This is the portion of weight of entering individual that is to be applied to based weight. The other weights are applied to initial free store (Weight 2-1) and initial propagule weight (Weight 2-2). For simplicity, determine the overall weight of an individual to enter and apportion weight across these three parameters (Weight 2-0, 2-1, 2-2).
Weight 2-1	initial free store/phloem	Portion of weight of entering individual devoted to free store energy
Weight 2-2	initial propagule weight	Portion of weight of entering individual devoted to reproduction. For plant, value = 0 at start of simulation if plant is initiated as a seedling.
Weight 2-3	initial pollen weight	For plant, initial weight of entering individual devoted to pollen production. Typically has a "0" value since plant is not pollinating initially.
Weight 2-4	energy producing ratio	Percent of plant mass that contributes to energy production.
Weight 2-5	cohort size	Refers to the number of individuals included in a super individual (not a super aphid). Super individuals differ from super aphids since they are mobile are not simultaneously developing and reproductive. Normal individuals should have a value of 1 for this parameter.

Table C.1. (continued) Initial traits input file key

Trait name Trait # - Parameter #	Parameter Description	Notes
Foraging 3-0	Foraging Radius	Delimits the area where an individual checks neighbors for potential trophic interactions. For these simulations, the value for plants was large in accordance with original developer advice to minimize interference of plant to plant competition.
Foraging 3-1	Relative Growth Rate	A plant only parameter used in plant growth and competition determination.
Foraging 3-2	Foraging Competition Weight	A plant only parameter relevant to plant to plant competition ability. It is used to calculate the amount of resources shared between plants covering the same area.
Dispersal rate 4-0	Dispersal, minimum distance	Minimum distance an immature or adult invertebrate can travel when prompted by starvation or competition. Appears to apply to invertebrates only.
Dispersal rate 4-1	Dispersal, maximum distance (adult)	Distance an adult invertebrate can travel when prompted by starvation or competition. Appears to apply to invertebrates only. (Dispersal 4-6 which applies to immatures)
Dispersal rate 4-2	Crowding: Min # of individuals	Minimum value assigned to plants representing the tolerance of plants to herbivores. Resulting values range from 0 to 1 with values approaching 1 causing herbivores to disperse from the overpopulated plants. Outputted as food competition.
Dispersal rate 4-3	Crowding: Max # of individuals	Maximum value assigned to plants representing the tolerance of plants to herbivores. Resulting values range from 0 to 1 with values approaching 1 causing herbivores to disperse from the overpopulated plants. Outputted as food competition.
Dispersal rate 4-4	Cost of dispersal	Energy cost of dispersal for invertebrates. Dispersal occurs when an individual is "stressed" by either lack of available food or due to food competition/crowding.
Dispersal rate 4-5	Probability of bouncing back	Probability that an individual will "bounce back" when it reaches the boundary of a patch (e.g., when dispersing). A value 1 results in a 100% chance of bouncing back.
Dispersal rate 4-6	Dispersal, maximum distance (larvae)	Distance an immature invertebrate can travel when prompted by starvation or competition. Appears to apply to invertebrates only. (Dispersal 4-6 which applies to immatures)
Immigration 5-0	Immigration	Assume closed system for now by original developers and the particular ability to incorporate immigration/emigration was not further explored for this project. Immigration ability is now enabled by the colonization input file and emigration could be enabled using the above probability of bouncing back parameter (Dispersal 4-5).
Reproduction 6-0	Weight of single propagule (egg or seed)	Single seed/egg weight Seed/egg batch size is captured. Together these two parameters determine the number of egg/seeds that can be released once sufficient propagule energy has been accumulated.
Reproduction 6-1	Weight ratio required to release seeds (Repro Ratio)	Releasing eggs/seeds after enough weight has been shunted to propagule production (i.e., propagule compartment). Individual reproductive Ratio of an individual's propagule weight to total weight required to release a batch of eggs/seeds. E.g., in the case of the plant, where 0.45 was assigned to this parameter, it releases seeds/eggs when 45% of total weight has been allocated to the propagule compartment. Set maize value to1.0 so plants held seeds.

Table C.1. (continued) Initial traits input file key

Trait name Trait # - Parameter #	Parameter Description	Notes
Reproduction 6-2	Max egg	Maximum number of eggs and adult invert can lay in a time step. Added for adults that do not feed but have a large amount of initial energy carried over from the larval/pupal stage. This parameter prevents the individual from releasing all of its eggs at once upon becoming an adult.
Reproduction 6-3	Max parasitoid eggs/larval host	Limit on number of eggs a parasitic wasp can lay per larval host.
Reproduction 6-4	Host preference	Indicates the functional type that a parasitoid attacks
Growth 7-0	Reproductive age dev state to adult (invert); switch to adult (plant)	Point at which plants become reproductive and energy begins to be shunted towards producing propagules. For plants, this is represented as number of days. Invertebrates are adults at this point and also begin shunting energy towards egg production. All invertebrate individuals are female. The value for adult invertebrates is 1.0.
Growth 7-1	Free Store to Base, FS2B	Ratio of base weight to free store weight for plants. Energy allocated to growth for invertebrates. Applies only to immature invertebrates since adults do not continue to grow. This is one of three parameters that influence invertebrate growth. The other two include the development constant (relates to developmental time) and food demand (relates to how quickly the individual accumulates mass).
Growth 7-2	Free Store to Propagule, FS2P	Energy allocated to propagule (seed/egg) production.
Growth 7-6	Free Store to Pollen (FS2Pol)	Energy shunted towards pollen production, e.g., 5% added to input file as 0.05
Growth 7-4	Time as pupae (days)	This is an invertebrate only parameter. Number of days spent as pupa. Invertebrates without a pupal stage (e.g., Hemiptera) have a value of zero for this parameter causing them to progress straight to the adult stage.
Growth 7-5	Total weight after pupa (%)	This is an invertebrate only parameter. Proportion of individual total weight remaining after the pupal stage. This allows a functional type to have an appropriate amount of weight reduced as it transitions from immature to adult stage.
Growth 7-3	Max weight	This is a plant only parameter that represents the maximum weight that the structural compartment can reach. Once max weight is reached a plant can continue to increase in weight as it adds propagule weight.
Growth 7-7	Pollen Age Span of Pollen Flow	Length of time (days) that pollen flows. Pollen initiates according to Growth 7-9.
Growth 7-8	Free Store to Adult	Percent of energy added from base weight to a new adult after pupation. The percentage is taken from the resulting adult weight after pupation (or after nymph stage). The purpose of this is to enable adults that do not feed or their food source is not present in the model (e.g., nectar) or adults that have limited feeding like lacewings that may only feed on pollen. This was important to add once adult feeding preference was added, one option of which is no feeding at all.

Table C.1. (continued) Initial traits input file key

Trait name Trait # - Parameter #	Parameter Description	Notes
Growth 7-9	Start pollination	Time step (day) when pollination is initiated. This allows variability to be added to pollination start to mimic variability that would be seen in the field. This is key for maize where pollen is an important food resource for some natural enemies.
Abundance 8-0	initial abundance	Number of individuals that enter each grid cell of a habitat patch. In the case of these simulations, this represents the number of individuals that enter 1 square meter.
Daily Food 9-0	Base daily food demand (db, Dbase)	Daily food demand is daily food requirement for an invertebrate individual at BaseTemp. If "Temp" from environmental parameters is equal BaseTemp (Daily Food 9-2) then food demand = db. The value is expressed as percent of total weight, i.e., 40% for aphid or 35% for predator. Value = 0 for plant.
Daily Food 9-1	Daily food demand increase with temp (dt)	The rate at which daily food requirements increase with Temp.
Daily Food 9-2	Base temp (TB)	Temperature that applies to daily food demand (9-0) as well as respiration (10-0).
Respiration 10-0	Base respiration cost (RB)	Respiration (metabolism) cost that an individual would have at base temp. Respiration cost expressed proportion of own weight. When Temp = Tempbase then RB = R. R=respiration cost which varies with temp and requires RT.
Respiration 10-1	Respiration cost increase with temp (RT)	Rate of increase of respiratory cost with temperature
Respiration 10-2	Unknown	Unknown. Values for this parameter are zero as received from original developers. This is not base temp for respiration since the code uses base temp from 9-2 (Tb from Daily Food Demand).
Biotype 11-0	General food preference	Identifies what given functional type eats, e.g., 0=detritus; 1=plants; 2=inverts. Currently, a functional type can feed on more than one of these by using the Preference tier and conversion rate matrix input files.
Development 12-0	Development constant (developB)	Growth rate that relates to the amount of time an invertebrate requires to reach pupation/adulthood. Individual daily development is devel = a + bT where a is a constant daily development and, b, the slope of the linear regression.
Development 12-1	Development Rate (developA)	Rate of growth rate change depending on temperature.
Development 12-2	Age	Age of individuals in days (or time steps) that are entering a simulation. The model is geared for adults entering, i.e., value of "1". This value also relates to survival probability (e.g., if the age is near the senescent age, then senescent daily mortality will soon be applied.

Table C.1. (continued) Initial traits input file key

Trait name Trait # - Parameter #	Parameter Description	Notes
Development 12-3	Development State	This determines the stage of the individual at the time it is introduced. This parameter works in conjunction with the above Development 12-2 parameter to determine the stage and age of entering individuals. A value of 1.0 results in adults entering. The model is geared towards adults entering.
Food Preference 13-0	Immature herbivore food preference	Herbivore food preference. A 0 value indicates that a herbivore/omnivore eats the entire plant (total weight); a "structure feeder" would be 1 (stalk weight); aphids feed on plant compartment 2, which is sap/free store; seed feeder is 3; pollen feeder is 4; 5 is leaf feeder.
Food Preference 13-1	Adult herbivore food preference	A 0 value is if a herbivore/omnivore eats the entire plant (total weight); a "structure feeder" would be 1 (stalk weight); aphids feed on plant compartment 2, which is sap/free store; seed feeder is 3; pollen feeder is 4; 5 is leaf feeder; 99= adults that do not feed.
N/A	Food handling time	This parameter was removed or not developed by the original developers since individuals have an entire time step (day) to acquire food. As a result, individuals were reasoned not to be limited by food handling times or affected by differential food handling times.

Table C.2. Complete list of modifications made to TrophicLINK to enable current project

Model Modification	Description
Pollen production	Pollen was a key change for this project since it is an important alternative food resource for many natural enemies. Plants were enabled to use a portion of their energy to produce pollen for a given amount of time. A pollination initiation time was added to allow for variable pollination start across plants.
Plant senescence	At the outset of the project, plants were being modeled using fresh weight. To accommodate this, plants would need to become senescent at some point later in the season. The initial idea was that this would also serve to simulate declining suitability of the plant as a host for insect pests, e.g., aphids. To address this, plants were made to begin to lose weight upon switch to senescence (Mortality initial trait 0-4) by a daily percentage set by a plant senescence rate parameter located in the environmental parameters input file. Later plants (and all functional types) were simulated using dry weight for simplicity sake. Plant senescence rate was set to zero. It is not clear from previous TrophicLINK publications whether the functional types were handled by dry or fresh weight (Caron-Lormier et al. 2009, Caron-Lormier et al. 2011).
Energy producing ratio for plants	The initial traits parameter, Weight 2-4, was added as an attempt to curb the energy production capability of plants. This trait was added to specifically targeted maize which grows very large causing it to be nearly impervious to insect damage.
Super aphid	Tracking extremely large numbers of individuals is computationally expensive and requires very long simulation times. Aphids quickly become abundant (e.g., into the millions) and cause run times to stretch into days. A super aphid individual was created since individual aphid dynamics is not a key aspect of the project. The importance of the presence of aphids is to provide a sporadically located food resource mass for natural enemies. A super aphid individual simultaneously grows and reproduces, is associated with a single plant when/if it successfully locates a host, and the population declines once it becomes senescent.
Super individual	Enabled by weight trait 2-5, cohort size, which allows for a single super-individual to contain multiple "sub-individuals". These individuals behave the same as a normal individual in that they are mobile and first grow and later become reproductive; however, they are associated with the same location. This is a method used in the literature to account for the computational problems associated with many individuals (Scheffer et al. 1995, Grimm et al. 2005).
Stalk borer	Stalk borers, such as the European corn borer, are protected from predation once they bore into the plant one day after egg hatch. Borers are available to natural enemies as a food resource only during the egg stage and for a day after egg hatch.
Predation size rule	The previous examples of TrophicLINK simulations included only small herbivores (aphids) and larger natural enemies. As a result, there was no issue with natural enemies being able to consume unrealistically large prey items. However, the current project included potential prey considerably larger than the predator/feeder. To account for this, a predation size rule was included that limited individuals from feeding on other individual invertebrates less than or equal to prey two times their own body weight.

Table C.2. (continued) Complete list of modifications made to TrophicLINK to enable current project[1]

Model Modification	Description
Food preference tiers	TrophicLINK initially had an interaction matrix input file including food preference linked with conversion rate. These two aspects of feeding were decoupled to allow for modification of food preference without having to scale the conversion rate.
Adult food preference	Adult invertebrates are enabled to have different food preferences than the immature stage. Examples where this is applied is for adult lepidopterans to not feed and allowing adult green lacewings to feed on pollen according to their realistic food preference. In practice, lacewing adults were also enabled to feed on aphids in order for them to survive and oviposit in scenarios without pollen (otherwise, they rapidly go extinct). Lepidopterans that do not feed require weight (i.e., energy) to be carried over from the larval stage (see initial traits parameter free store to adult.
Free store to adult	Initial traits growth parameter 7-8 allows a percentage of larval weight to be carried over to the adult stage. This is required for non-feeding adults which otherwise would quickly starve as adults since they have no way of obtaining energy.
Max egg	Adults that do not feed and carryover energy from the larval stage have a large amount of energy available for producing eggs when they become adults. The maximum number of eggs that can be laid in a day (initial trait, reproduction 6-2) prevents these adults from releasing all of their eggs in a single day. Through reverse parameterization, adults can be limited to oviposition of a realistic numbers of eggs per day.
Invertebrate dispersal	Added an additional maximum dispersal distance parameter to accommodate both immature and adult dispersal distances.
Consumption Mass Output	An additional output file was added to report the amount of a given food item that a trophic-functional type consumed. This is referred to as predation mass within the code.
Larval Parasitoid	A larval parasitoid functional type was developed that attacks larvae of a certain invertebrate.

Table C.3. Life history measurements of European corn borer, Ostrinia nubilalis, reared at 25 ºC[1]

Rep	Late instar mass (mg)	Pupal mass (mg)	Adult mass (mg)	Egg cluster mass (mg)	# eggs/ cluster	Single egg mass (mg)	1st instar larvae group mass (mg)	# larvae/ group (mg)	Mass/single 1st instar larvae (mg)
1	100.8	98.6	20.4	0.6402	15	0.0427	0.9	28	0.0321
2	133.4	83.2	41.9	1.452	32	0.0454	2.7	70	0.0386
3	185.2	94.2	22.2	0.495	11	0.0450	3.4	96	0.0354
4	211.4	83.4	41.6	n/a	n/a	n/a	n/a	n/a	n/a
5	167.9	99.6	42.9	n/a	n/a	n/a	n/a	n/a	n/a
6	117.2	95	33.9	n/a	n/a	n/a	n/a	n/a	n/a
7	171.1	116.7	27.5	n/a	n/a	n/a	n/a	n/a	n/a
8	120.4	96.1	31	n/a	n/a	n/a	n/a	n/a	n/a
9	143.3	65.2	36.7	n/a	n/a	n/a	n/a	n/a	n/a
10	113	120.1	26.3	n/a	n/a	n/a	n/a	n/a	n/a
11	159	99.4	20.3	n/a	n/a	n/a	n/a	n/a	n/a
12	120.5	82.4	n/a	n/a	n/a	n/a	n/a	n/a	n/a
13	112.6	108.4	39.9	n/a	n/a	n/a	n/a	n/a	n/a
14	117.4	123.5	21.2	n/a	n/a	n/a	n/a	n/a	n/a
15	130.9	129.4	33.6	n/a	n/a	n/a	n/a	n/a	n/a
16	128.1	151.7	42.6	n/a	n/a	n/a	n/a	n/a	n/a
17	172.5	198.2	22.5	n/a	n/a	n/a	n/a	n/a	n/a
18	165.4	84.7	24.7	n/a	n/a	n/a	n/a	n/a	n/a
19	160.6	156.3	31.7	n/a	n/a	n/a	n/a	n/a	n/a
20	107.4	129.21	45.2	n/a	n/a	n/a	n/a	n/a	n/a
21	205.4	107.1	34.2	n/a	n/a	n/a	n/a	n/a	n/a
22	210.8	188.5	36.7	n/a	n/a	n/a	n/a	n/a	n/a
23	132.5	175.4	38.1	n/a	n/a	n/a	n/a	n/a	n/a
Mean	147.3	116.8	32.5	n/a	19.3	0.0443	n/a	n/a	0.0354
SD	34.2	34.9	8.1	n/a	11.2	0.0015	n/a	n/a	0.0032

[1] Measurements were conducted during summer of 2015 at Monsanto Company research facilities in St. Louis, Missouri, by Angela Martin and Joshua Uffman. Insects were obtained from Monsanto-Union City facility (Union City, TN). Insects were fed multiple species diet (Southland Products, Inc., Lake Village, AR). Incubation occurred in Percival environmental chambers (Model 136VL, Percival Scientific, Perry, IA). Insects were weighed using Mettler balance model XS204 (Mettler-Toledo, Columbia, MD).

Table C.4. Developmental measurements of European corn borer, *Ostrinia nubilalis*, reared at 25 ºC

Indiv	Pupation (day)	Eclosion (day)	Pupal duration (days)	# individuals pupating each day (Day/#indivs)	# individuals eclosing each day (Day/#indivs)
1	16	29	13	Day 16, 3	Day 10, 5
2	18	28	10	Day 17, 4	Day 11, 4
3	17	27	10	Day 18, 8	Day 12, 5
4	18	30	12	Day 19, 2	Day 13, 4
5	18	30	12	Day 20, 2	Day 14, 1
6	18	31	13	Day 21, 1	Day 15, 0
7	17	28	11	Day 22, 1	Day 16, 2
8	24	34	10	Day 23, 1	Day 17, 1
9	18	29	11	Day 24, 1	Day 18, 0
10	16	36	20	n/a	Day 19, 0
11	19	29	10	n/a	Day 20, 1
12	17	29	12	n/a	n/a
13	18	29	11	n/a	n/a
14	23	35	12	n/a	n/a
15	16	29	13	n/a	n/a
16	20	30	10	n/a	n/a
17	18	34	16	n/a	n/a
18	20	33	13	n/a	n/a
19	18	32	14	n/a	n/a
20	17	33	16	n/a	n/a
21	21	32	11	n/a	n/a
22	19	36	17	n/a	n/a
23	22	34	12	n/a	n/a
Median	18	30	12	n/a	n/a

[1] Measurements were conducted during summer of 2015 at Monsanto Company research facilities in St. Louis, Missouri, by Angela Martin and Joshua Uffman. Insects were obtained from Monsanto-Union City facility (Union City, TN). Insects were fed multiple species diet (Southland Products, Inc., Lake Village, AR). Incubation occurred in Percival environmental chambers (Model 136VL, Percival Scientific, Perry, IA). Insects were weighed using Mettler balance model XS204 (Mettler-Toledo, Columbia, MD).

Table C.5. Life history measurements of fall armyworm, *Spodoptera frugiperda*, reared at 25 ºC

Rep	Late instar mass (mg)	Pupal mass (mg)	Adult mass (mg)	Egg cluster mass (mg)	# eggs/ cluster	Single egg mass (mg)	1st instar larvae group mass (mg)	# larvae/ group (mg)	Mass/single 1st instar larvae (mg)
1	236	240.8	113.8	1.5976	31	0.0515	3.2	102	0.0314
2	282.4	298.8	95	0.2893	5	0.0579	2.7	82	0.0329
3	275.3	265.2	122.3	0.8154	16	0.0510	1.4	44	0.0318
4	298.9	240.2	108	n/a	n/a	n/a	n/a	n/a	n/a
5	282.2	236.3	123.4	n/a	n/a	n/a	n/a	n/a	n/a
6	264.2	239.9	128.3	n/a	n/a	n/a	n/a	n/a	n/a
7	284.1	260.7	102.7	n/a	n/a	n/a	n/a	n/a	n/a
8	289.7	266.3	98.8	n/a	n/a	n/a	n/a	n/a	n/a
9	272.8	252	168	n/a	n/a	n/a	n/a	n/a	n/a
10	294.3	264	114.1	n/a	n/a	n/a	n/a	n/a	n/a
11	256.5	247.3	131.9	n/a	n/a	n/a	n/a	n/a	n/a
12	301.9	270.9	144.4	n/a	n/a	n/a	n/a	n/a	n/a
13	301.9	250.5	124.7	n/a	n/a	n/a	n/a	n/a	n/a
14	285.1	297.4	138.7	n/a	n/a	n/a	n/a	n/a	n/a
15	277.2	244.2	142	n/a	n/a	n/a	n/a	n/a	n/a
16	275.5	271.9	130.8	n/a	n/a	n/a	n/a	n/a	n/a
17	289.3	241	100.1	n/a	n/a	n/a	n/a	n/a	n/a
18	268.6	289.7	114.1	n/a	n/a	n/a	n/a	n/a	n/a
19	267.4	256.4	138.9	n/a	n/a	n/a	n/a	n/a	n/a
20	293.8	233.5	138.2	n/a	n/a	n/a	n/a	n/a	n/a
21	278.3	247.6	140.1	n/a	n/a	n/a	n/a	n/a	n/a
22	248.3	230.9	128.8	n/a	n/a	n/a	n/a	n/a	n/a
23	286.8	274.4	143.6	n/a	n/a	n/a	n/a	n/a	n/a
Mean	278.7	257.4	125.7	n/a	17.3	0.0535	n/a	n/a	0.0320
SD	16.6	19.7	18.0	n/a	13.1	0.0038	n/a	n/a	0.0008

[1] Measurements were conducted during summer of 2015 at Monsanto Company research facilities in St. Louis, Missouri, by Angela Martin and Joshua Uffman. Insects were obtained from Monsanto-Union City facility (Union City, TN). Insects were fed multiple species diet (Southland Products, Inc., Lake Village, AR). Incubation occurred in Percival environmental chambers (Model 136VL, Percival Scientific, Perry, IA). Insects were weighed using Mettler balance model XS204 (Mettler-Toledo, Columbia, MD).

Table C.6. Developmental measurements of fall armyworm, *Spodoptera frugiperda*, reared at 25 ºC

Indiv	Pupation (day)	Eclosion (day)	Pupal duration (days)	# individuals pupating each day (Day/#indivs)	# individuals eclosing each day (Day/#indivs)
1	17	26	9	Day 16, 7	Day 8, 2
2	17	27	10	Day 17, 9	Day 9, 9
3	21	30	9	Day 18, 3	Day 10, 6
4	16	25	9	Day 19, 1	Day 11, 3
5	17	27	10	Day 20, 1	Day 12, 1
6	16	31	15	Day 21, 1	Day 13, 1
7	23	34	11	Day 22, 0	Day 14, 0
8	16	25	9	Day 23, 1	Day 15, 1
9	16	27	11	n/a	n/a
10	16	24	8	n/a	n/a
11	20	30	10	n/a	n/a
12	17	27	10	n/a	n/a
13	17	26	9	n/a	n/a
14	16	26	10	n/a	n/a
15	16	29	13	n/a	n/a
16	18	27	9	n/a	n/a
17	18	27	9	n/a	n/a
18	17	25	8	n/a	n/a
19	17	29	12	n/a	n/a
20	17	26	9	n/a	n/a
21	17	26	9	n/a	n/a
22	19	29	10	n/a	n/a
23	18	29	11	n/a	n/a
Median	17	27	10	n/a	n/a

[1] Measurements were conducted during summer of 2015 at Monsanto Company research facilities in St. Louis, Missouri, by Angela Martin and Joshua Uffman. Insects were obtained from Monsanto-Union City facility (Union City, TN). Insects were fed multiple species diet (Southland Products, Inc., Lake Village, AR). Incubation occurred in Percival environmental chambers (Model 136VL, Percival Scientific, Perry, IA). Insects were weighed using Mettler balance model XS204 (Mettler-Toledo, Columbia, MD).

Table C.7. Life history measurements of four species of lady beetles (Coleoptera: Coccinellidae)[1]

Lady beetle	Measurement	Egg weight (mg)	First instar larvae (mg)	Late instar larval weight (mg)	Pupal weight (mg)	Adult weight (mg)
A. bipunctata	1	0.138	0.143	n/a	15.1	11.1
	2	0.139	0.157	n/a	11.8	9.8
	3	0.133	0.150	n/a	12.8	10.2
	4	0.129	0.120	n/a	15.5	12.5
	5	0.140	0.100	12.6	n/a	8.8
	6	n/a	0.109	13.9	n/a	10.5
	7	n/a	n/a	21.2	n/a	n/a
	8	n/a	n/a	16.7	n/a	13.5
	9	n/a	n/a	14.9	n/a	11.3
	10	n/a	n/a	20.4	n/a	13.8
	11	n/a	n/a	16.3	n/a	13.2
	12	n/a	n/a	13.9	n/a	11.4
	13	n/a	n/a	n/a	n/a	14.0
	14	n/a	n/a	n/a	n/a	13.7
	15	n/a	n/a	n/a	n/a	11.1
	16	n/a	n/a	n/a	n/a	15.3
	17	n/a	n/a	n/a	n/a	16.8
	18	n/a	n/a	n/a	n/a	17.4
	19	n/a	n/a	n/a	n/a	22.7
	20	n/a	n/a	n/a	n/a	11.0
C. septempunctata	1	0.291	0.240	n/a	n/a	44.7
	2	0.206	0.230	n/a	n/a	55.7
	3	n/a	0.213	n/a	n/a	41.5
	4	n/a	n/a	n/a	n/a	49.5
C. transversalis	1	0.244	n/a	42.2	30.7	27.8
	2	0.260	n/a	34.2	37.7	33.5
	3	0.255	n/a	38.5	34.6	30.3
	4	0.225	n/a	45.0	40.7	36.0
	5	n/a	n/a	39.6	35.1	36.0
	6	n/a	n/a	35.4	30.8	27.3
	7	n/a	n/a	n/a	n/a	43.0
	8	n/a	n/a	n/a	n/a	50.1
	9	n/a	n/a	n/a	n/a	41.0
	10	n/a	n/a	n/a	n/a	59.5
	11	n/a	n/a	n/a	n/a	29.5
	12	n/a	n/a	n/a	n/a	33.4
H. convergens	1	n/a	n/a	n/a	n/a	25.2
	2	n/a	n/a	n/a	n/a	24.7
	3	n/a	n/a	n/a	n/a	32.3

[1] Lady beetles included *Adalia bipunctata*, *Coccinella septempunctata*, *Coccinella transversalis*, and *Hippodamia convergens*. All were field collected from Montana State University campus and, where applicable, maintained under ambient conditions in the lab. Ambient conditions consisted of approximately 24/22 °C day/night temperatures. Eggs and early instars were weighed in groups and single egg/larva weight was determined by dividing by the number of individuals per group. Eggs of *A. bipunctata* and *C. transversalis* that were monitored hatched in 4-5 days. Pupal stage duration of *A. bipunctata* and *C. transversalis* was approximately 5 days. Shaded cells indicate that the measurements were taken on the same individual.

C.8. Late instar, pupal, and adult weight measurements of the cabbage white butterfly, *Pieris rapae* (Lepidoptera: Pieridae)[1]

Individual	Late instar weight (mg)	Pupal weight (mg)	Adult weight (mg)
1	148.8	135.6	68.7
2	166.3	124.8	50.0
3	170.3	148.7	64.5
4	155.5	134.3	67.0
5	145.7	135.7	n/a

[1] Data were collected in support of lepidopteran pest parameterization, specifically late instar weight measurements and weight reduction from late instar and pupal weights relative to adult weights. Caterpillars were field collected from swiss chard and reared on the same plant under ambient conditions (approximately 24 °C). Data were not available for adult weight of individual 5 since this individual died during eclosion.

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