

**Effects of landscape, field management, and abiotic conditions  
on soybean arthropod community composition and ecosystem services**

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**Thesis Abstract**

A growing body of literature over the past two decades has examined how landscape composition and structure affect communities and processes in agroecosystems, including crop pests and their natural enemies. A few general patterns have emerged: the diversity and abundance of natural enemies increases as noncrop habitat increases and landscapes have been found to have strong impacts on natural enemies' biological control ability. However, many relationships remain unclear: landscape composition can affect natural enemy species, guilds, or trophic levels differently and there is no consistent relationship between landscape complexity and crop pests. Improving models of landscape heterogeneity impacts on agricultural insect community abundance and composition could give more insight into these patterns.

Landscape characteristics are not the only factors impacting crop yields though. There are many non-landscape factors, such as abiotic conditions, that are known to influence insect pests and natural enemies in agroecosystems. Temperature and precipitation are known to directly and indirectly affect insects in agroecosystems, and like landscapes, are heterogeneous across time and space. Across large geographic areas, the combination of landscape composition gradients and environmental gradients, such as temperature and precipitation, be difficult to disentangle. Thus my objectives were to determine the contribution of landscapes and abiotic factors to crop pest and natural enemy abundance in Wisconsin soybean fields and to assess the contribution of landscapes, abiotic factors, and pesticide use on ecosystem services, such as conservation biological control and crop yields, in Wisconsin soybean fields through impacts on crop pests and natural enemies.

First, I used ecoinformatic approaches and model averaging to examine the effects of landscape context, growing degree days, and precipitation on midseason soybean aphid abundance. The results indicate that soybean aphids are responding strongly to precipitation patterns and growing degree days, as well as land use. Second, I use ecoinformatic approaches and generalized additive models to examine the effects of landscape, growing degree days, and drought stress on the abundance and diversity of generalist predators of soybean aphids. While results were taxon specific, they indicate the importance of including biotic drivers, like pest densities, in addition to landscape and abiotic factors, when studying patterns in natural enemy presence and abundance. Third, I used experimental clip-cage assays to test biological control potential of soybean aphid predators under ambient predation conditions. These results show that biological control potential was influenced by prey densities, as well as interactions between growing degree days, predator abundance, grassland in the landscape, further demonstrating the importance of understanding variation in land use and climatic conditions together. Lastly, I used a two-tiered sampling approach to test the effects of landscape context, growing degree days, and insecticide use to predict field-scale soybean yields. Soybean yields are positively correlated with corn and grassland in the landscape, as well as insecticide use in the surrounding county, while being negatively correlated with growing degree day accumulation.

As a whole, this work contributes to our understanding of landscape context as a driver of insect abundance and function in agroecosystems, by incorporating alternate possibilities and potential covarying mechanisms. I was successful in tracing landscape effects to crop yields, as the first study we know of to accomplish this at field-scales. I found that both crop and noncrop habitats in the landscape support increased yields, as well as increased natural enemy occurrence and

abundance in soybean fields. Yet the heterogeneous responses of specific taxa to landscape features, combined with the strong response of predator abundance and biological control potential assays to prey density, indicates that explicitly tracking resources within the growing season, rather than static annual metrics of land cover, may be a better way of understanding the contribution of landscapes. Additionally, soybean aphids appeared to benefit from increasing forest acreage in the landscape. Yet pest populations were more strongly correlated with abiotic factors, specifically precipitation and growing degree days, indicating that explicit inclusion of non-landscape factors is critical. Across large geographic areas and multiple years, disentangling the contributions of landscape composition gradients and environmental gradients can be difficult. This dissertation is evidence that taking on that challenge resulted in exploration of landscape effects I am more confident in and can question further.

## **Thesis Introduction**

Agriculture in the United States has been consolidated and intensified in the past fifty years. There is increasing pressure on fewer farmers to produce increasing yields on fewer farms, characterized by large land parcels and high inputs. These patterns have altered plant and animal communities and ecological processes within individual fields and cumulatively affected agricultural landscapes. Intensified agriculture has been linked to decreases in ecological functioning and biodiversity (Polis et al. 1997, Thies and Tschardtke 1999, Poggio et al. 2013). Local species richness in agroecosystems has also been linked to the surrounding landscape (Marino & Landis 1996, Weibull et al. 2000).

Understanding changes in agricultural landscapes is critical for society, as they provide critical provisioning ecosystem services including food for people and animals, fiber, fuel, and pharmaceuticals (Power 2010). Thus a growing body of literature over the past two decades has examined how landscape composition and complexity affect agroecosystem communities and processes, including crop pests and their natural enemies. For example, the diversity and abundance of insect predators and parasitoids are often higher in areas with a greater proportion of noncrop, “semi-natural” area in the vicinity (Bianchi et al. 2006, Thies et al. 2005, Landis et al. 2000). Consequently, in areas with more non-crop land, the ability of entomophagous arthropods to consume pest insects is generally higher (Werling et al. 2011, Thies and Tschardtke 1999), potentially leading to reduced crop damage (Liere et al. 2015).

Other relationships between landscape structure and crop pests are not yet understood. For example, a recent meta-analysis found landscape complexity does not show consistent patterns

with crop pest abundance (Chaplin-Kramer et al. 2011). And while there is some evidence that landscape effects can cascade down to crop yields (e.g., Liere et al. 2015), most studies have extrapolated findings from very small spatial scales (Liere et al. 2015) or very small sample sizes (e.g., Ostman et al. 2003).

Improving models of the effects of landscape heterogeneity on agricultural insect community abundance and composition is not enough though. Landscape characteristics are not the only factors impacting crop insects and ecosystem services. Abiotic conditions, including temperature and precipitation, directly and indirectly affect insects in agroecosystems, and like landscapes, are heterogeneous across time and space. As poikilothermic organisms, insects are especially sensitive to variability in temperature (Parmesan 2007). Sudden changes in habitat moisture or temperature often kill insects (Schowalter 2011). Rainfall can impede insect dispersal and dislodge them from host plants (Thackray et al. 2004). Understanding climatic gradients is even more critical in studies specifically interested in landscapes, as the spatial extent is large enough that variation in abiotic conditions can be expected. Landscapes and abiotic conditions might co-vary; so research to understand the drivers of crop pest and natural enemy abundance in agricultural landscapes would benefit from the inclusion of abiotic conditions.

Within-field management is also critical to understanding yield patterns. Farming practices vary widely between farms and across regions, including seed variety and planting dates, fertilizer and nutrient management, pesticide applications, and whether fields are rainfed or irrigated. Research in agricultural landscapes often means conducting research on working farms, which may be using pesticides to maximize yields and profits. Yet studies on these farms are often categorized

in a false dichotomy of organic versus conventional, which ignores the complex interactions that the application of chemicals, dose, timing, frequency, and toxicity may have with nontarget insects and organisms in the agroecosystem. Thus studies conducted in agricultural landscapes would also benefit from the explicit inclusion of nuanced measurements of pesticide use and other pest management practices in models of crop pests and natural enemies.

Thus, in an effort to determine the effect of “landscapes” on crop pest and natural enemy abundance in Wisconsin soybean fields, I set out to assess the contribution of landscape structure, abiotic factors, and pesticide use on crop insect pests and their natural enemies in Wisconsin soybean fields. First, I examined the effects of landscape context, growing degree days, and precipitation on midseason soybean aphid abundance using ecoinformatic approaches and model averaging. Second, I examined the effects of landscape, growing degree days, and drought stress on the abundance and diversity of generalist predators of soybean aphids using a large observational dataset and generalized additive models. Third, I tested biological control potential of soybean aphid predators under ambient predation conditions using experimental clip-cage assays. Lastly, I tested the effects of landscape context, growing degree days, and insecticide use on field-scale soybean yields using a two-tiered sampling approach and linear mixed models.

The soybean (*Glycine max*) agroecosystem in Wisconsin is a good system for answering these questions. Soybean is a leguminous crop plant widely grown in the eastern and north central regions of the United States. In 2013, 75.7 million acres of soybeans were grown in the United States, with 1.58 million of those grown in Wisconsin by thousands of farmers (USDA NASS). The soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae]) is a critical soybean

insect pest in Wisconsin and in the North Central region of the United States. Aphid feeding on the leaves, stems, and pods of soybean causes direct damage to plants via reduced photosynthesis, plant growth, and yield (Ragsdale et al. 2007). Generalist predators, especially ladybird beetles, have been shown to play a key role in suppressing soybean aphid populations in its new range (Costamagna and Landis 2006, Costamagna et al. 2007, Costamagna et al. 2008). Previous research indicates that both soybean aphids and their generalist predators are influenced by landscape composition and complexity (Gardiner et al. 2009, Gardiner et al. 2009b, Mitchell et al. 2014). Soybean is a food and fuel crop grown for human consumption, animal feed, and biodiesel due to its high oil content. Addressing my landscape questions in the soybean agroecosystem is not only interesting ecologically, but provides an opportunity to develop applied results that could improve conservation biological control and crop yields in this important crop that continues to grow in acreage worldwide.

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## Chapter 1

### **Explicit modeling of abiotic and landscape factors reveals precipitation and forests associated with aphid abundance**

#### **Abstract**

Increases in natural or non-crop habitat surrounding agricultural fields have been shown to be correlated with declines in insect crop pests. However, these patterns are highly variable across studies suggesting other important factors, such as abiotic drivers, which are rarely included in landscape models, may also contribute to variability in insect population abundance. The objective of this study was to explicitly account for the contribution of temperature and precipitation, in addition to landscape composition, on the abundance of a widespread insect crop pest, the soybean aphid (*Aphis glycines* Matsumura), in Wisconsin soybean fields. We hypothesized that higher soybean aphid abundance would be associated with higher heat accumulation (e.g., growing degree days), and increasing non-crop habitat in the surrounding landscape, due to the presence of the overwintering primary hosts of soybean aphid. To evaluate these hypotheses, we used an ecoinformatics approach that relied on a large dataset collected across Wisconsin over a 9-year period (2003 – 2011), for an average of 235 sites per year (n=2,110 fields total). We determined surrounding landscape composition (1.5-km radius) using publicly available satellite-derived land cover imagery and interpolated daily temperature and precipitation information from the National Weather Service COOP weather station network. We constructed linear mixed models for soybean aphid abundance based on abiotic and landscape explanatory variables and applied model averaging for prediction using an information theoretic framework. Over this broad spatial and temporal extent in Wisconsin, we found that

variation in growing season precipitation was positively related to soybean aphid abundance, while higher precipitation during the non-growing season had a negative effect on aphid populations. Additionally, we found that aphid populations were higher in areas with proportionally more forest, but were lower in areas where minor crops, such as small grains, were more prevalent. Thus, our findings support our hypothesis that including abiotic drivers increases our understanding of crop pest abundance and distribution. Moreover, by explicitly modeling abiotic factors, we may be able to explore how variable climate in tandem with land cover patterns may affect current and future insect populations, with potentially critical implications for crop yields and agricultural food webs.

## Introduction

Arthropods in agricultural fields can be affected by the composition and configuration of the surrounding landscape. For example, the diversity and abundance of insect predators and parasitoids are often higher in areas with a greater proportion of noncrop, “semi-natural” area in the vicinity (Bianchi et al. 2006, Thies et al. 2005, Landis et al. 2000). Consequently, in areas with more non-crop land, the ability of entomophagous arthropods to consume pest insects is generally higher (Werling et al. 2014, Thies and Tschnartke 1999), with effects cascading to lower crop damage (Liere et al. 2015) and with lower broad-scale pesticides used to prevent economic losses (Meehan et al. 2011, Meehan and Gratton 2015). Yet, in contrast to generally consistent patterns found with insect predators and parasitoids, recent reviews examining the relationship between landscape attributes and insect herbivore (i.e., crop pest) abundance have found less consistent relationships (Veres et al. 2013, Chaplin-Kramer et al. 2011). In some cases, insect herbivore abundance is negatively correlated with increasing non-crop habitat, while other studies find it to be positively correlated. This variation in response complicates attempts to manage agricultural landscapes to conserve and promote entomophagous natural enemies while suppressing insect crop pests without pesticides.

There are several possible contributing factors to the heterogeneous responses of insect herbivores to landscape composition. One is the lack of consistent inclusion of explanatory factors other than landscape characteristics. Previous modeling attempts often only include landscape characteristics of interest as predictors (e.g., Liere et al. 2015). Yet, not including other variables that may be correlated to landscape characteristics could possibly lead to an overestimate of the importance of landscape effects as the drivers of insect populations. For

example, temperature is negatively correlated with latitude at coarse scales, and temperature is known to impact the survival, development rate, growth, and fecundity of herbivorous insects. Some studies examining landscape and pest relationships attempt to account for such patterns by assessing spatial autocorrelation of model residuals (Gardiner et al. 2009a). However, even if those approaches improve model fits or patterns of residual variation, it is difficult to ascribe the direct relationship between these unmodeled variables and insect populations. Therefore, the inclusion of abiotic factors in studies of insect herbivore abundance across landscapes may account for some of the range in crop pest responses to landscape characteristics.

Abiotic conditions, such as temperature and moisture are known to affect insect physiology and behavior. As poikilothermic organisms, insects are especially sensitive to variability in temperature (Parmesan 2007), which is why degree-day based models have long been used to predict the emergence and growth of insect pests (Wilson and Barnett 1983). Long-term exposure to increased temperatures can result in desiccation if body water content falls too low, and dehydration can fatally decrease body water and metabolic rates (Hadley 1994). Similarly, variation in precipitation and moisture availability may have both direct and indirect effects on insect herbivores. Sudden changes in habitat moisture or temperature often kill insects (Schowalter 2011). Rainfall can impede aphid dispersal (Thackray et al. 2004) and dislodge aphids from host plants, potentially leading to mortality from impact, predation, or starvation (Winder 1990). When plant water demand is greater than the supply from precipitation and soil moisture storage, host plant water content is reduced, which in turn may cause drought stress in insect herbivores (Kennedy et al. 1958).

Given these well established relationships, it is surprising that abiotic factors have generally not been explicitly included in landscape-dependent models of insect abundance in agricultural contexts, though several studies have explicitly acknowledged a lack of research that examines how landscapes and abiotic factors contribute to crop pest populations (e.g., nutrient stress, Noma et al. 2010; temperature, Benton et al. 2002). Studies outside of agricultural systems, in contrast, such as those examining invasive insects and insect vectors of pathogens, have taken a more pluralistic approach and incorporated both abiotic and landscape characteristics as explanatory factors to understand variation in insect populations (Trotter et al. 2013, Ruiz et al. 2010). Other modeling approaches, such as occupancy modeling and climate envelope modeling do explicitly account for climatic and other abiotic variables, but often exclude landscape variables as potential explanatory variables. For example, Araújo and Luoto (2007) used bioclimatic envelope models to explore butterfly populations and tested whether biotic interactions impacted distributions, yet did not include habitat, landscape or other geographic factors. Conversely, climate model approaches are not widespread in landscape models of insect abundance, perhaps due to the potential complexity of interpreting both landscape and abiotic factors.

Interpreting the role of abiotic factors in changes to insect crop pest populations at landscape scales may be difficult. When working across large geographic areas, the effect of location may combine the effects of gradients in both landscape characteristics and temperature and precipitation, thus making it difficult to interpret the actual causal factors underlying variation in insect populations. Careful modeling of spatial autocorrelation patterns may account for some of the variation across geographic gradients that is not attributable to land cover or

compositional patterns that may be attributable to abiotic factors (Meehan and Gratton 2015).

While this allows a clearer interpretation of land cover effects on animal abundance, it partitions variability into random effects (e.g., spatial lag effects) that are difficult to interpret.

Our objective in this study was to determine the contribution of landscape composition, as well as temperature, and precipitation on mid-season soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae], hereafter SBA) abundance in Wisconsin. The soybean aphid is a key pest of soybean (*Glycine max*), which causes stunting in plants, yellowing and curling of leaves, and ultimately lowers seed yield from direct feeding (Ragsdale et al. 2007) and indirectly through virus transmission (Mueller et al. 2010). Previous studies suggest that SBA abundance is positively associated with increasing non-crop habitats of agricultural landscapes (Bahlai et al. 2008, Gardiner et al. 2009, Gardiner et al. 2009b, Gardiner et al. 2010, Woltz et al. 2012). A multiyear study of SBA found oscillating population cycles (Rhainds et al. 2010), which the authors attributed to predator-prey dynamics with ladybird beetle predators (Coccinellidae), suggesting additional factors may also contribute to variation in SBA populations. In fact, higher diversity and abundance of generalist predators of SBA are sometimes associated with increasing proportions of grasslands and other non-forested semi-natural habitat in the landscape (Gardiner et al. 2009b; Woltz et al. 2012) potentially resulting in increased biological control of insect pests (Werling et al. 2012, Werling et al. 2011). Moreover, the SBA is a host-alternating aphid with its primary host, buckthorn (*Rhamnus* spp.) common in the forest understory in Wisconsin woodlands (soybean is the secondary summer host of SBA; Ragsdale et al. 2004). In the spring, alate (winged) SBA leave woodlots to colonize emerging soybean plants, where they have multiple parthenogenic generations in the summer before

returning to buckthorn for the sexual and overwintering generation. Thus, the composition of the landscape, both through its potential effect on the colonization dynamics of soybeans, and through the effect on aphid natural enemies could play an important role in explaining the dynamics and abundance of SBA in agricultural landscapes. Given the likely roles of landscape and abiotic factors on aphid abundance, we explicitly aimed to model both effects to understand their relative contributions to the abundance of SBA in Wisconsin. Specifically, we hypothesized that (1) higher growing season precipitation would result in more soybean aphids, as more rainfall could increase soil moisture and improve host plant quality for phloem feeders (Zehnder et al. 2009), (2) increased temperatures would result in more soybean aphids, since developmental rates are often found to be positively associated with increases temperature for SBA (McCornack et al. 2004), and (3) that increased forest cover in the vicinity of soybean fields would be positively associated with abundance due to the common presence of buckthorn, the overwintering hosts of SBA, in Wisconsin forests (Rogers et al. 2008).

By combining analyses of the effects of abiotic drivers (temperature and precipitation) and landscape composition to understand SBA populations, we can develop a better understanding of the unique and relative contribution of these factors on the abundance of this crop pest. Moreover, by explicitly modeling abiotic factors, we create new possibilities of modeling pest populations under the combined instance of both land cover and climate changes.

## **Methods**

### *Soybean aphid counts*

Between 2003 and 2011, we counted soybean aphids in 2,110 soybean fields across Wisconsin (Fig. 1, Appendix Fig. 1). Each site was only visited once during each of the 9 years of the study ( $250 \pm 23$  different sites / year), and fields were not revisited in subsequent years. Fields were visited between June 27 and August 24 in each calendar year, with July 27 being the average sampling date, corresponding to when SBA abundance has historically been near peak for the growing season (Mitchell et al. 2014a). At each site, we entered the field from the roadside edge at a randomly selected location along the edge. We counted all the soybean aphids on 5 plants at four different stations (at the corners of a 20 x 20 m square), a minimum of 50 m from the edge of the field, for a total of 20 whole-plant counts per field. This sampling method was used to match the standard practice for SBA monitoring by growers, crop scouts, and extension professionals (e.g. Ragsdale et al. 2007). We recorded the soybean growth stage of each plant examined (Licht 2014). We recorded all aphid counts and calculated the average number of soybean aphids per plant for each site. Average aphid counts per site was  $\log_{10}(x+1)$  transformed prior to analysis to normalize residuals.

### *Landscape composition*

We collected location data at each sampling site with hand-held GPS receivers. We determined the landscape composition around each sampling site using satellite-derived land cover imagery from the National Land Cover Database (NLCD) (MRLC 2003-2010) and the United States Department of Agriculture's Cropland Data Layer (CDL) (USDA NASS 2003-2011). We imported annual land cover maps into ArcGIS (v.10, ESRI 2011), and extracted the proportions of each land cover attribute within a 1.5 km radius buffer circle of each GPS coordinate. We selected aggregated landscape composition classes and our spatial scale of interest based on

previous research indicating relevance to soybean aphids and their natural enemies (Gardiner et al. 2009a). To correct for low attribute accuracy in early years of the CDL for non-crop habitats, we substituted in non-crop habitat pixels of the CDL with NLCD values, using NLCD 2001 data for our 2003 – 2005 samples and NLCD 2006 data for our 2007-2010 samples. We aggregated raw land cover classes into proportions of the landscape using the following categories: soybean, corn, other agriculture, forest, grassland, water, wetlands, and developed/urban. Aggregating landscape composition categories from the raw land cover classes was also done to increase land cover prediction accuracy, which varies widely for individual crops, grassland types, and forest types, especially in the earlier years of this analysis (USDA NASS Cropland Data Layer Metadata <http://www.nass.usda.gov/research/Cropland/metadata/meta.htm>). “Other agriculture” included all annual (not including soybean and corn) and perennial non-grassland crops, such as small grains, alfalfa, and beans. “Forest” included deciduous, evergreen, and mixed forests. “Grassland” included both managed (e.g., pasture) and natural (e.g., restored prairie) grasslands. “Developed/urban” included residential and industrial land uses. Statistical analyses included soybean, corn, other agriculture, forest, and grassland as “landscape” predictors of aphid abundance.

#### *Temperature and Precipitation*

Daily temperature and precipitation data for all operational weather stations in Wisconsin from November 2002 through December 2011 were obtained from the National Climatic Data Center portal (<http://www.ncdc.noaa.gov/>). We identified the weather station nearest to each sampling site reporting daily maximum and minimum temperatures for inclusion, for a total of 444 weather stations averaging a distance of 6.2 miles from sampling sites (Appendix Fig. 1). When

necessary, we filled in missing daily weather station data by taking the average of the missing measurement on the same date from all other weather stations in the same climate reporting district (Serbin and Kucharik 2009).

We consider the effect of temperature on SBA abundance using cumulative growing degree days. Cumulative growing degree days (GDD) measure heat accumulation throughout the calendar year, expressed in GDD units. We used the basic method equation, taking the average of the daily minimum and maximum temperatures compared to a base temperature (McMaster and Wilhelm 1997). We used a base temperature of 4.4 °C for SBA, based on empirically-derived temperature thresholds in the Midwest US (Cantangui et al. 2009). For each sampling site, we calculated GDD from January 1<sup>st</sup> of the year through the date of aphid sampling.

We calculated two precipitation metrics for each sampling site and date. The first, “non-growing season precipitation”, was the cumulative precipitation in millimeters from the previous November 1<sup>st</sup> through April 30<sup>th</sup> of the sampling year at a given site. This metric captures the amount of precipitation at sites that has fallen after the previous year’s harvest but before soybeans are planted in the sampling year and therefore before SBA can be present on soybean. Soil moisture storage and groundwater recharge increases as precipitation increases during this time period, potentially resulting in reduced plant stress during the growing season (Sacks et al. 2010). The second precipitation-related measure, “growing season precipitation”, was the cumulative precipitation in millimeters from May 1<sup>st</sup> of the sampling year through the sampling date at each site. This metric captures the amount of precipitation that has fallen during the growing season, and can be directly experienced by SBA (e.g. physical disturbance) and soybean plants (e.g. changes in plant quality). Increased growing season precipitation could result in

reduced plant stress, with higher quality foliage potentially supporting higher SBA populations (Zehnder et al. 2009). Conversely, acute periods of high precipitation in the growing season could physically dislodge aphids and potentially result in lower insect populations through increased mortality events (Chaplin-Kramer et al. 2013). Overall, we anticipated the net effect of growing-season precipitation to be positively associated with SBA abundance.

### *Statistical analysis*

To understand the relationship between landscape, abiotic variables, and SBA abundance we used multi-model inference based on the bias-corrected Akaike Information Criterion (AIC<sub>c</sub>) (Richards 2005). We fit linear mixed-effects models with log-transformed average aphid abundance as our response variable, and landscape variables (proportions of soy, corn, other crops, grassland, and forest) and abiotic variables (GDD, non-growing season precipitation, and growing season precipitation) as fixed effects. As random effects in the model, we included year, soybean plant growth stage, and year by land cover interactions for corn, soy, grassland, other crops, and forest to account for inter-annual variability in land cover effects on SBA abundance. A spatial correlation term using latitude and longitude was also included to account for potential autocorrelation between aphid measurements between sites that were closer to each other and to improve the model fit by accounting for other spatial variability not accounted for in the fixed effects. The best fitted model for this spatial correlation structure was based on semivariograms using the *gstat* package in R (Pebesma and Graeler 2015). Therefore, fixed effects can be interpreted as the unique partial contributions of each factor independent of other factors, while accounting for other unexplained spatial structure in the data. In order to improve computational performance and compare the direction and magnitude of fixed effects, we

centered and scaled all independent variables before analysis (Gelman 2008). Then, we used the *dredge* and *model.avg* functions from the MuMIn package (Barton 2014) written for R statistical computing software (R Development Core Team 2008) to rank all possible subsets of the full model using  $AIC_c$ , calculate model weights, and compute variable importance weights and model-averaged coefficients (Burnham and Anderson 2002). Model averaging builds uncertainty into independent variable parameter estimates, producing unconditional estimates of variances. This approach represents a focus on estimating general relationships and effect sizes, and acknowledging model uncertainty given correlated variables, as opposed to conducting multiple null hypothesis tests and choosing a single best model (Burnham and Anderson 2002). The inclusion of interactions of landscape and abiotic factors with year is an effort to examine general relationships between the fixed effects and SBA across the duration of the study, rather than predict aphid abundance in any one specific year.

Of all possible subsets, models in the top 95% based on ranking of their  $AIC_c$  scores were retained as the candidate set of models. From this candidate set of models, we calculated model-averaged coefficients as weighted average values, where weighting was based on relative  $AIC_c$  scores, to achieve a single model-averaged model (Burnham and Anderson 2002). Variable relative importance weights, which range from 0 to 1, were based on the sum of the  $AIC_c$  scores in all the candidate models in which a particular independent variable occurred. We examined model fits using a pseudo  $R^2$  calculated, determined by squaring the correlation of our observed data with the fitted model predictions for each data point, and root mean square error (RMSE). We assessed model residuals using spline correlograms, using the *ncf* package in R (Bjornstad

2013) and found little spatial autocorrelation (Appendix Fig. 3), and the spatial autocorrelation structure was the same in both the combined and landscape-only model.

## Results

SBA populations varied greatly between sampling years, with 2003 having the highest annual mean density of 768 aphids per plant (SD=878, IQR=487.97) compared to 2010 when plants had mean aphid densities of just 2 per plant (SD=39, IQR=0.42, Fig. 1). The variability in non-growing season precipitation, and growing season precipitation during this period was within the range of historical precipitation experienced in the state between 1980 and 2009 (Appendix Fig. 2).

Model-averaging results suggested that growing season precipitation had the strongest (most positive) and most consistent (highest variable-importance weight) association with SBA abundance (Fig. 2). The proportion of forest cover within 1.5 km radius of a sampling site also had positive and consistent association with SBA abundance. Additionally, we found non-growing season precipitation and the proportion of “other crops” (agricultural acreage other than corn or soy) was negatively correlated with SBA abundance and had high variable-importance weights, indicating that they occurred in a large fraction of the best models (Fig. 2). The only other variable showing a possible association with SBA abundance (importance values > 0.5) was GDD, but the direction of its relationship was not consistent across models, as seen in the error bars intersecting zero (Fig. 2). Our model-averaged model fit appeared to vary by observation year (Appendix Fig. 4), due to the large variation in SBA populations across years (Fig 1). Examination of the interannual variation of the slopes of the fixed effects in our

combined model-averaged model revealed that the effects of non-growing season precipitation and forest acreage with SBA abundance were generally large across the study period (Fig. 2), the relationship was highly variable across years (Appendix Fig. 5).

Comparing the combined model with the landscape-only model revealed that a landscape-only model had similar coefficient sizes and no difference in the direction of relationship of SBA abundance with the landscape-based fixed effects (Table 1) with similar model fits (combined model, RMSE 0.533, pseudo- $R^2 = 0.65$ , compared to landscape-only model, RMSE 0.534, pseudo- $R^2 = 0.64$ , Table 1). The difference between the two approaches to understanding SBA abundance is evident not by the overall fit of the models, but by the contribution of the abiotic factors to the combined model (Table 1, Figure 2).

## **Discussion**

Although landscape associations with insects are becoming widely reported (Chaplin-Kramer et al. 2011), they are generally discussed in absence of other known gradients, such as temperature and precipitation that could also have effects on their populations. Using an ecoinformatics and model-averaging approach, we found that a combination of landscape characteristics and abiotic variables explained variability in populations of this herbivore. Specifically, spatial variation in precipitation had significant effects on SBA abundance with increasing precipitation within the growing season having generally positive associations with SBA, while increases in non-growing season precipitation had a negative effect. Both of these findings suggest either indirect effects of soil moisture on aphids through their effects on plant performance, or direct effects of precipitation on survivorship of these insects. Consistent with

the host-alternating life history of the aphid, we also found that increasing forest cover in the landscape around fields was associated with larger SBA populations, likely due to the common presence of buckthorn in Wisconsin forests (Rogers et al. 2006). Our explicit inclusion of abiotic factors gives us more confidence in SBA associations with the landscape characteristics tested.

Our large scale temporal and spatial dataset allowed us to detect the average effects of landscape, temperature and precipitation on aphid populations, even with large interannual variability in SBA population densities (Fig. 1) and in potential climatic drivers (Appendix Fig. 5). Interestingly, the “landscape-only” model performed as well as the combined model with both landscape and abiotic variables (e.g., similar model fits and model coefficients). This suggests that the additional variation explained by the abiotic variables was being adequately accounted for by the spatially-dependent autoregressive random effects in the landscape-only models; in fact, both models have little spatial structure remaining in the residuals and the spatial autocorrelation structure was similar in both models (Appendix Fig. 3). By explicitly including climatic variables into the aphid abundance models, we were able to extract variability that was previously only accounted for in the spatial terms. Included as fixed effects in the combined model, we now have a better understanding of how variability in climate affects aphid abundance and have the capacity to explicitly explore these effects on aphids, which before was not possible since abiotic effects were subsumed within the random error terms.

#### *Landscape effects on SBA*

As expected based on the life-history of SBA, we found increasing amounts of forest cover in the vicinity of aphid sampling was strongly positively correlated with SBA abundance (Fig. 2). We hypothesize that the mechanism for this pattern is the likely presence of buckthorn (*Rhamnus* spp.) in forests. Buckthorn is SBA's primary host and an understory tree commonly found in forests across Wisconsin (Rogers et al. 2006, Voegtlin et al. 2005). Soybean fields surrounded by greater amount of forest habitat could have higher SBA populations due to movement off buckthorn and onto soy at the beginning of the growing season. Bahlai et al. (2008) found that soybean aphid density is positively correlated with the density of buckthorn plants in the vicinity of soybean fields in Canada. Yet, a more recent study found SBA relationships with forest could not be attributed to buckthorn presence or abundance (Mitchell et al. 2014a) and a similar study found SBA abundance to be lowest near forest patches (Mitchell et al. 2014b). However, the researchers only measured SBA populations in 2010 and 2011, the two years in our study with the lowest SBA populations, suggesting that source colonization effects may be more likely to be observed in higher aphid years. While these relationships may be true within the specific sampling years, we focused our study and analysis on broad patterns found across our 9 year dataset. In fact, our models showed significant interannual variability in the effect of forest on SBA abundance (Appendix Fig. 5), suggesting that, although generally positive (Fig. 2), this effect is highly variable among years of the study, making it difficult to generalize the effects of forest from studies of only 1-2 years duration. Nevertheless, the strong association between the amounts of forest in the vicinity of soybean fields suggests that there may be specific areas in the landscape where the need for soybean aphid control measures may be more likely.

We also found SBA abundance to be negatively correlated with the increased presence of agricultural crops other than corn and soy (Fig. 2). This result supports previous research that suggests other crops, which, although they do not support SBA development since this aphid is host-specific to soybeans, could be source habitats for generalist natural enemies that also prey on soybean aphid in nearby soybean fields (Gardiner et al. 2009b; Woltz et al. 2012). Thus, this non-soybean crop agricultural land, rather than noncrop habitat, may be critical to supporting SBA predators due to prey switching. Similarly, Liere et al. (2015) found that soybean aphid natural enemies were more common as the proportion of overall cropland neighboring soybean fields increased. As the growing season progresses, generalist predators of SBA such as ladybird beetles move around agricultural landscapes tracking available prey resources, including aphids (Elliott et al. 2002). It's likely that other crops, such as alfalfa and winter wheat, provide them with food resources earlier in the season, before SBA aggregations are sufficient to attract predators. We did not find a consistent relationship of SBA abundance with proportions of corn, soy, or grassland in the surrounding landscape (Fig. 2). This result is in contrast to previous findings that soybean aphid densities were negatively correlated with increasing non-forested, non-crop habitat (Noma et al. 2010). Non-crop habitat was recently found to be positively correlated with abundance of other aphid species (Plecas et al. 2014), and positively correlated with biological control of other insects (Werling et al. 2012, Werling et al. 2011). Thus, natural enemy population variation may be better explained by the availability of alternate prey and source potential, rather than solely on the presence of non-crop vegetation cover (Elliott et al. 2002).

#### *Abiotic effects on SBA*

Although this study is a first using SBA-specific GDDs in combination with landscape composition to understand soybean aphid abundance in fields across space (i.e., statewide) for multiple years, we did not find clear evidence that variation in temperature affected SBA abundance. Recent experiments with pea aphids found that while warmer temperatures did increase their population growth rate, the overall effect on abundance varied depending on their predators' response to the warming (Barton and Ives 2014b). Therefore, to understand the net effects of temperature on aphids may require a more complete understanding of the broader community including predators which interact with aphids.

On the other hand, variability in precipitation did affect aphid abundance. Increased precipitation which occurred during the period of soybean growth was associated with higher aphid densities possibly due to both direct and indirect effects of precipitation on SBA abundance. Relatively wetter conditions during the growing season may increase plant growth and enhance plant quality (Zehnder et al. 2009), which may in turn facilitate the increase of aphid populations. Sufficient precipitation during the growing season is critical for optimal soybean growth, although the benefit of the total precipitation is reduced if received via extreme weather events, which result in less usable water for the plants (Hatfield et al. 2010). A recent study examining 40 years of soybean yields in the Midwest US also found an association between precipitation, resulting available water, and yield variability (Egli and Hatfield 2014). While irrigation may be a possible solution to improving yield gaps, our research suggests that improving water availability may also make plants more attractive to herbivores.

Other research on aphid abundance has found a negative relationship between precipitation and aphid densities (Chaplin-Kramer et al. 2013, Merrill and Peairs 2012, Cocu et

al. 2005). Those studies hypothesize that rain may physically dislodge aphids from plants and cause direct mortality or may increase predation rates on the ground. However, since SBA generally were more abundant when growing season precipitation was higher, this could argue that natural enemies may be doing worse in wetter conditions. This idea would run counter to the prevailing data, which suggests that aphid populations early in the season may be susceptible to entomopathogenic fungi that are relatively more effective in wetter conditions (Koch et al. 2010). However, a recent experiment simulating reduced precipitation in alfalfa found that altered predator behavior in the system was responsible for significantly higher spotted aphid abundance (Barton and Ives 2014a) suggesting that natural enemies in this system may not have consistent responses to summer precipitation.

In contrast, increasing precipitation in the non-growing season portion of the year (November – April) was associated with lower mid-growing season SBA abundance. Wetter winters are often associated with delayed spring planting of crops (Sacks et al. 2010). This could result in later soybean phenology, possibly delaying emergence and growth until after early season SBA colonization. Additionally, it is possible that increased non-growing season precipitation directly impacts SBA migration and movement from buckthorn onto soybean hosts in the spring. A recent study examined the possibility that SBA overwinter in states south of Wisconsin and move north in the spring, despite a higher prevalence of buckthorn in Wisconsin (Crossley and Hogg 2015). However, it's difficult to tease this pattern apart, as the precipitation data examined in our study is associated with our sampling sites, not the likely overwintering sites in different states. It is notable that the effect of non-growing season precipitation on aphid abundance was highly variable among years, potentially reflecting the complex interactions

between cool and wet springs on soybean planting time and the subsequent effects on pest populations.

### *Ecoinformatics modeling of landscape and abiotic factors*

We capitalized on a large dataset of crop pest records from commercial soybean fields in Wisconsin, and used an ecoinformatics approach to explore the possible drivers of SBA abundance in these fields. An advantage of this ecoinformatics approach that includes many one-time observations across such spatial and temporal breadth is a greater statistical power to explore broad scale patterns that may manifest as small effects (Meisner and Rosenheim 2014). The model selection process that explored candidate models with all possible combinations of variables to explain aphid abundance resulted in a model-averaged model that includes both abiotic and landscape factors. While this study is only a snapshot of SBA abundance during the growing season, we have included samples across a broad spatial extent across many growing regions in the state and over a 9 years period. This is in contrast to many studies investigating landscape effects on pests and pest control which typically have a more narrow geographic range (Gardiner et al. 2009, Noma et al 2010) but are more temporally resolved (Chaplin-Kramer et al. 2011). The use of multi-year analyses has the potential to increase the conditions under which particular drivers become important, and allows for more generalizable conclusions regarding the effects of particular variables on animal abundance (Chaplin-Kramer et al. 2013; Schmidt and Tscharrntke 2005).

Our large, observational dataset and ecoinformatics approach has inherent drawbacks that can be complemented by smaller, experimental studies (Rosenheim and Meisner 2013). The

dataset lacked site-specific knowledge of factors that could affect aphids. For example, the use of preventative pest suppression practices (e.g., pesticide use) to manage pests and ensure high yield and income returns likely varies across the sites sampled in this study (e.g., Meehan et al. 2011). Within-field variables could also further explain soybean aphid densities and be included in future, improved models of soybean aphid population patterns. Lower potassium concentrations in soybean leaves and soil have been shown to increase soybean aphid densities (Myers et al. 2005, Myers and Gratton 2006). Crop rotations and land use legacies can also influence aphid densities by altering plant nutrient availability (Noma et al. 2010). The presence of non-soybean plants in fields and along field margins, such as in-season ground cover and edge plantings, could also influence aphid populations directly by providing habitat like buckthorn, or indirectly by augmenting resources for natural enemies (Schmidt et al. 2008; Bahlai et al. 2008). As it stands, although these factors may be important in affecting aphid abundance, they are currently part of the random (unexplained) variation in the model. Future efforts could be aimed at including additional factors that may further explain aphid abundance patterns across the landscape.

### *Conclusions*

Understanding changes in agricultural landscapes is critical for society, as these landscapes provide services that benefit people by sustaining ecological functions, such as pollination, natural pest suppression, and nutrient and water cycling (Power 2010). Our analysis of crop pest populations from soybean fields in the upper Midwestern USA, along with previous research, suggests that changes in landscape composition can affect SBA presence and abundance. However, our analysis also indicates that non-landscape factors, specifically precipitation, are

important for modeling crop pest populations. Even after accounting for several random effects with a large but noisy observational dataset, we found strong signals.

Given that herbivores are sensitive to environmental characteristics such as landscapes and climate characteristics, future land use change (de Araújo et al. 2015) and changes in temperature and precipitation will likely also alter crop pest distribution and abundance (Bebber et al. 2013). Downscaled global circulation model output indicates that Wisconsin's fall, winter, and spring precipitation, as well as year-round temperature, will increase due to climate change (WICCI 2011). As our study indicates that increasing precipitation's effect on SBA depends on whether that rainfall is during the growing season, it is unclear how future rainfall patterns in Wisconsin will impact this pest population. The significance of the impact of abiotic factors combined with landscape characteristics is not limited to SBA or crop pests. Recent research on West Nile Virus (*Flavivirus*) indicates that changes in the timing and amount of rainfall and heat accumulation in the past decade resulted in measurable changes in infection rates, yet the directionality of that change varied across landscapes (Hahn et al. 2015). Thus, understanding how these relationships may change given uncertain future climatic conditions has critical implications for human health, as well as agricultural ecosystems. Future research on insect crop pests in agricultural landscapes should include abiotic and landscape factors, to increase our understanding of the mechanisms driving presence, abundance and spatial patterns of SBA and other pests in the present and into the future.

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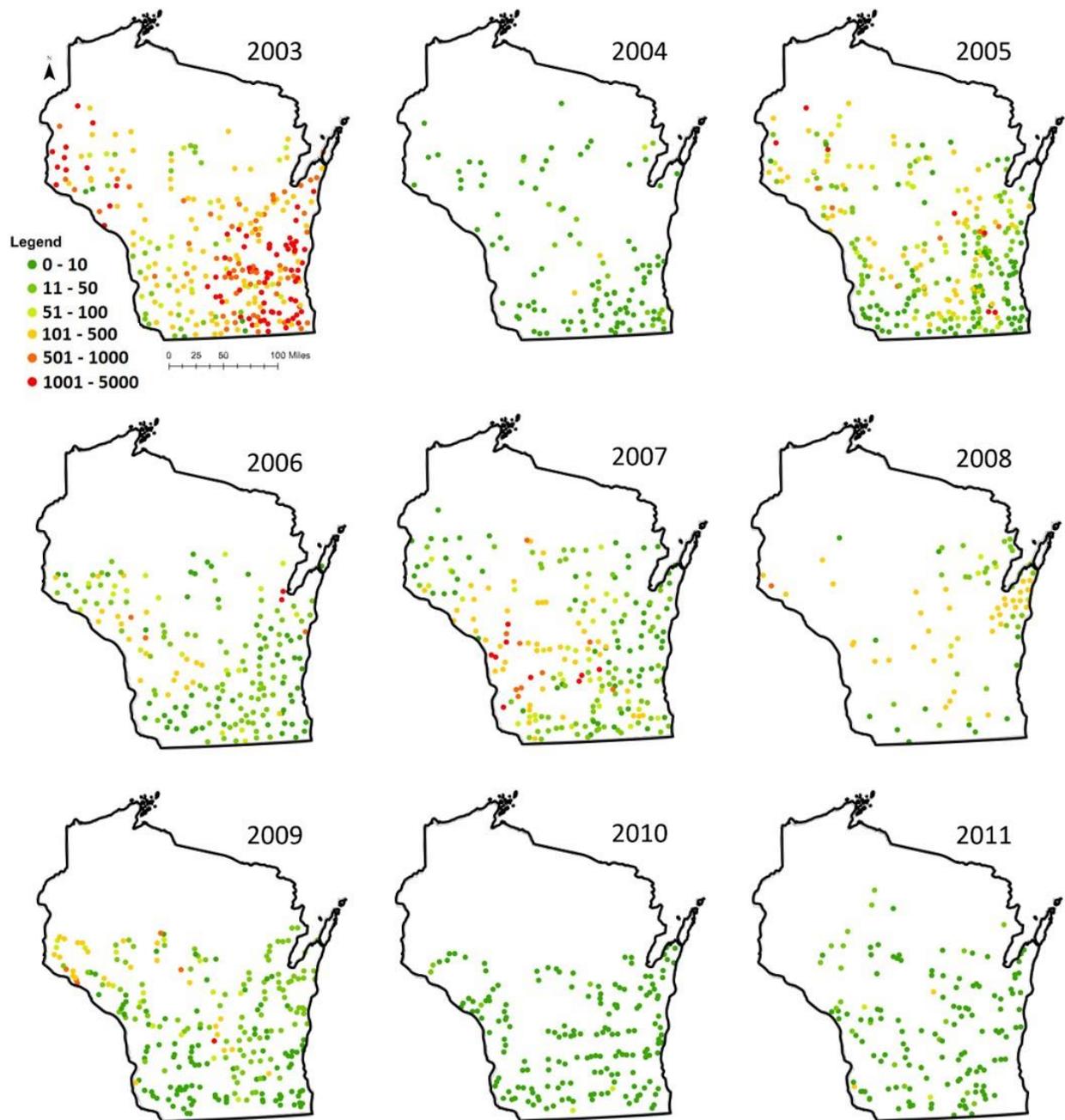
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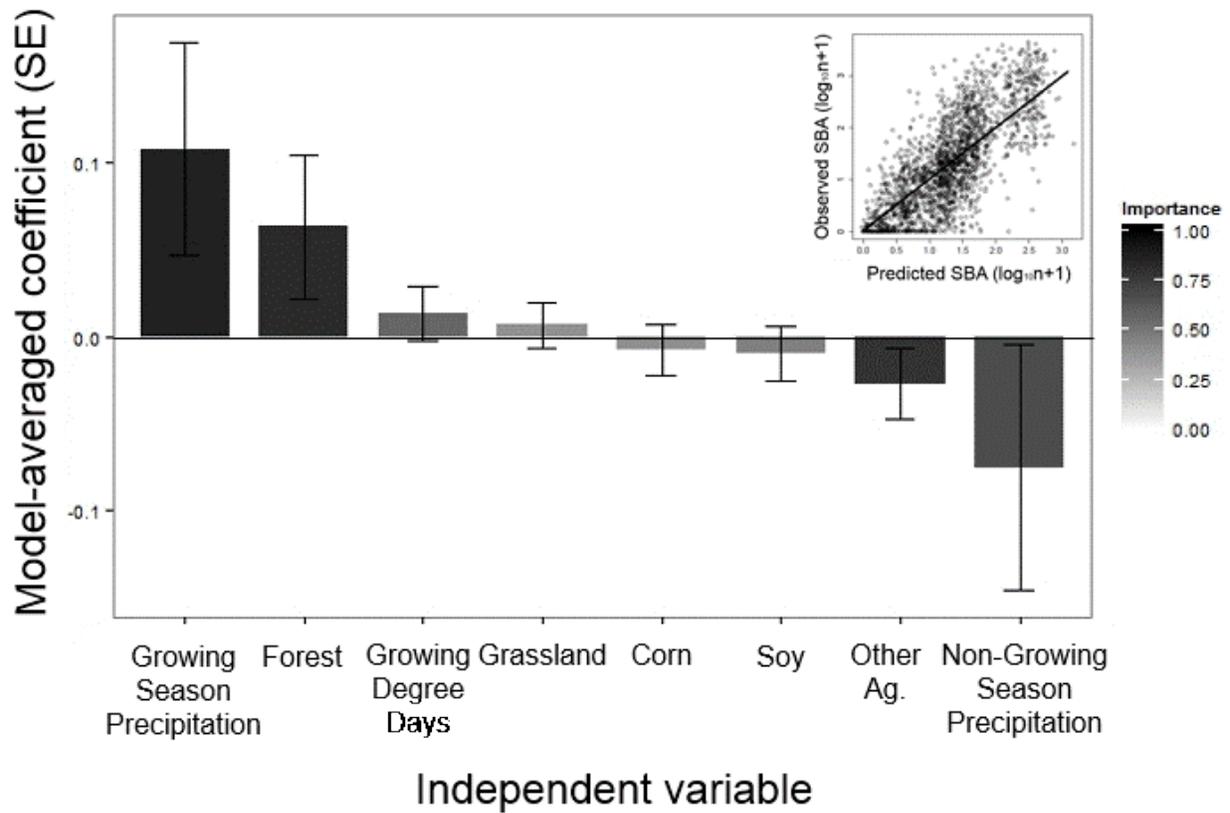
**Table 1.** Model-averaged coefficients (standard error) of the combined model and landscape-only model fitted to soybean aphid (*Aphis glycines*) abundance ( $\log_{10} x+1$  transformed), surveyed in Wisconsin between 2003 – 2011. The models include all the same fixed landscape and random effects terms, but the landscape-only model omits the growing degree days, non-growing season precipitation, and growing season precipitation terms.

	Landscape and Abiotic	Landscape only
	Coefficient (SE)	Coefficient (SE)
Landscape variables		
Forest	0.0633 (0.0415)	0.0644 (0.0417)
Grassland	0.00673 (0.0133)	0.00772 (0.0141)
Corn	-0.00754 (0.0147)	-0.00955 (0.0161)
Soy	-0.0100 (0.0156)	-0.00863 (0.0150)
Other crops	-0.0272 (0.0203)	-0.0258 (0.0200)
Abiotic variables		
Growing season precipitation	0.108 (0.0617)	
Growing Degree Days	0.0132 (0.0155)	
Non-growing season precipitation	-0.0757 (0.0707)	
	<sup>a</sup> Pseudo-R <sup>2</sup> 0.654	0.645

<sup>a</sup> Measured by squaring the correlation of our observed data with the fitted model predictions.

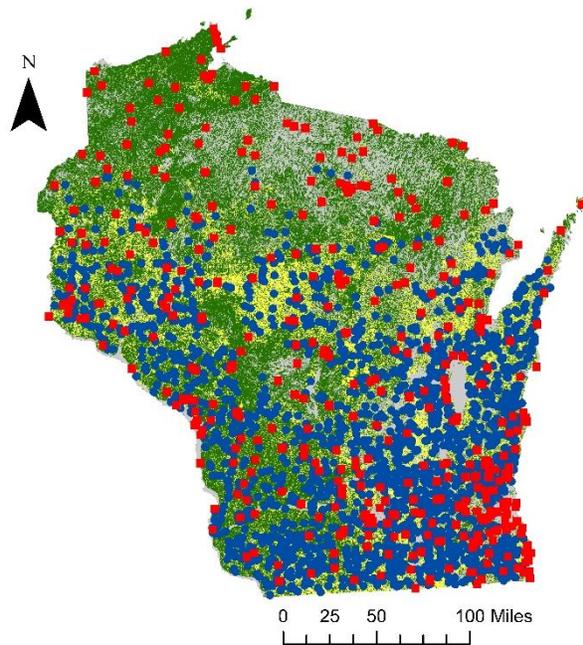


**Figure 1.** Observed average soybean aphid abundance per plant at the 2,110 sampling locations (points) across Wisconsin between 2003 and 2011. Northern one-third of the state is mostly forested and has few soybean fields (see Appendix Fig. 1).

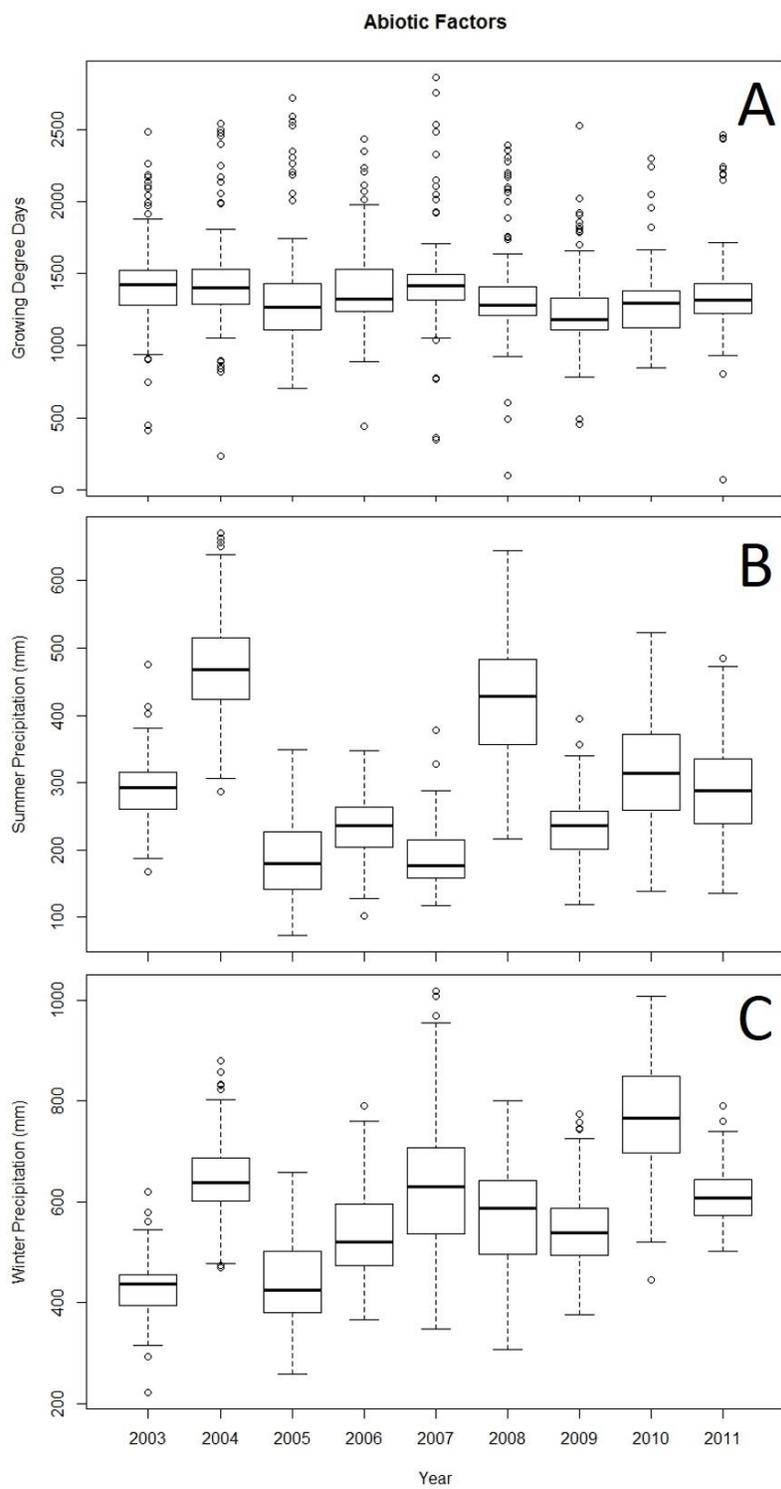


**Figure 2.** Mean effect size ( $\pm$ SEM) of the independent fixed variables in our best model derived from model averaging predicting soybean aphid abundance at sites in Wisconsin, USA, between 2003 and 2011. Darker shaded bars indicate higher variable importance weight (i.e., higher cumulative AIC scores of the models that included this variable). The model predicted values (inset) had a squared correlation with observed data values of 0.65 (pseudo- $R^2$ , line is a 1:1).

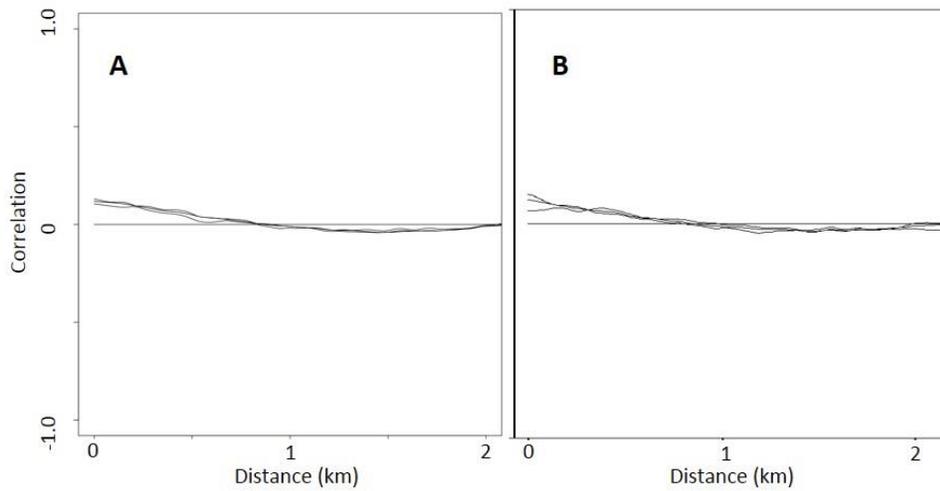
## Supplemental Appendices



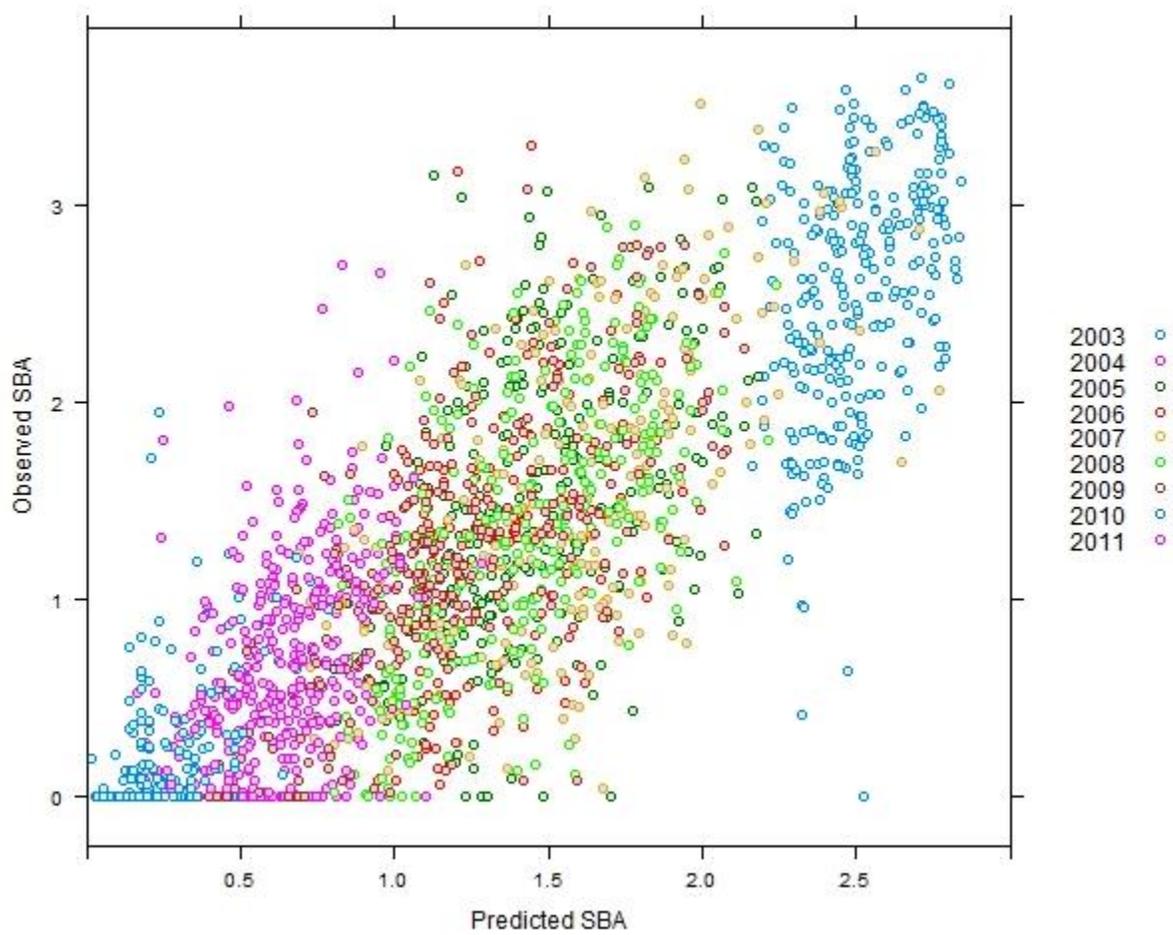
**Appendix Figure 1.** Blue dots show the spatial distribution of the 2,110 soybean fields in Wisconsin where we counted soybean aphids between 2003 and 2011 for this study. Red dots show the 444 weather stations in Wisconsin operating between November 1, 2002 and December 31, 2011 included in this study and reporting daily temperature and precipitation data available through the National Climate Data Center (NCDC 2014). The sites and station locations are overlaid on a map of the 2011 USDA Cropland Data Layer (USDA), with yellow pixels representing all annual agriculture, green pixels representing forest and grassland, and grey pixels representing landcover categories not included in this study (wetland, urban, and water).



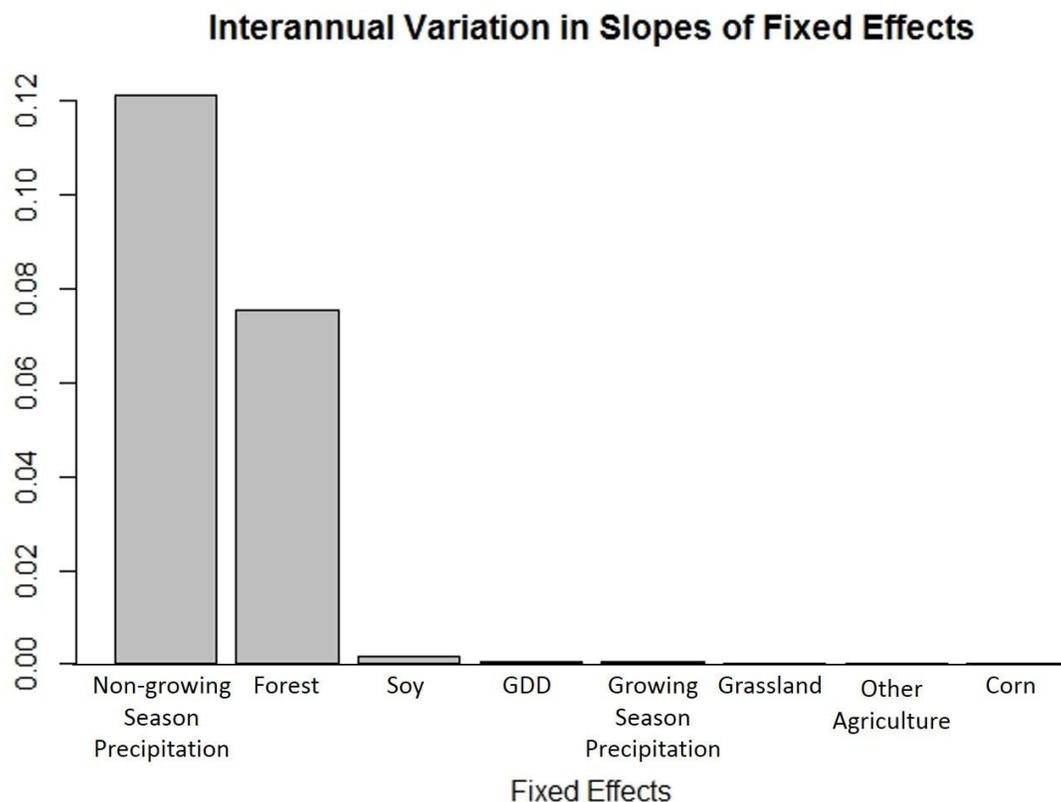
**Appendix Figure 2.** Box plots of (A) growing degree days (GDD), (B) non-growing season precipitation (November 1 of the previous year through April 30 of the sampling year), and (C) growing season precipitation (May 1 through the sampling date) for all sampling sites by year.



**Appendix Figure 3.** Model residuals using spline correlograms from the ncf package in R for (a) our combined (landscape+abiotic) model-averaged model and (b) our landscape-only model-averaged model.



**Appendix Figure 4.** Predicted log transformed soybean aphid abundance (SBA) values at each sampling site versus observed log transformed SBA values at each site, color coded by observation year.



**Appendix Figure 5.** The interannual variation in slopes of the fixed effects of our combined model-averaged model, as measured by the standard deviation of the random effects in our model. The fixed effects named specific land cover categories (forest, soy, grassland, corn, other agriculture) refer to the proportion of that land cover in the 1.5-k radius area around the sampling sites. The fixed effects named ‘non-growing season precipitation’ (November 1 of the previous year through April 30 of the sampling year) and ‘growing season precipitation’ (May 1 through the sampling date) refer to the cumulative precipitation at the nearest weather station to a sampling site, while ‘GDD’ refers to the cumulative growing degree days at the nearest weather station to a sampling site.

## Chapter 2

### **Generalist predator responses to landscape composition, abiotic conditions, and prey availability in Midwest US soybean agroecosystem**

#### **Abstract:**

Previous research on landscape composition effects on agroecosystem natural enemies supports the positive association between noncrop habitat and natural enemy abundance and diversity. Yet these studies often fail to include abiotic factors, which have known important direct and indirect effects on natural enemy survival, foraging, and plant-insect interactions. Thus the goal of this study was to examine how including abiotic conditions and prey availability could change interpretations of landscape composition relationships with agroecosystem insect communities in soybean (*Glycine max*). We collected generalist predator insects using sweep sampling in 1,082 soybean fields across Wisconsin in 2010 through 2014. At each site, we determined landscape composition around the field, growing degree days, and drought stress, and prey (*Aphis glycines*) densities on soybean plants. We analyzed our data using generalized additive models (GAMs) with natural enemy abundance as our response variable as a function of landscape and abiotic factors and their interactions.

Our results show that models of natural enemy community abundance and diversity that include abiotic factors and biotic interactions perform better than those that only use landscape variables or do not include spatial autocorrelation terms. Our analysis of generalist natural enemy community data from soybean fields in the Midwest US suggests that changes in landscape composition do affect soy natural enemy presence and community composition. However, the specific habitats and direction of those relationships depends on the taxonomic group of interest – as well as other critical non-landscape drivers, including temperature, moisture availability,

and prey density. Overall, our study demonstrates the importance of also including abiotic and biotic factors when examining relationships between landscape composition and natural enemy communities. Understanding natural enemy relationships with temperature and drought stress will be increasingly important when predicting future effects due to climate change.

### **Introduction**

Insect natural enemies can provide critical natural pest suppression services in agroecosystems. Their ability to act as biological control of crop pests on farms is in part determined by the structure and composition of the surrounding landscape (Marino and Landis 1996, Thies et al. 2003, Tscharrntke et al. 2005). Other landscape variables that impact biological control by insect natural enemies include patch size, habitat quality, habitat complexity, and organisms' dispersal ability (Thies et al. 2003). Natural enemies may also take advantage of off-farm locations for favorite microclimates conducive to oviposition or larval development. Additionally, many natural enemies are generalist predators that can switch prey and consume crop derived resources found in the landscape surrounding farm fields. Understanding the relationship between natural enemies and landscape composition in agricultural landscapes is important, as the availability of resources in these landscapes can be important for conserving natural enemies.

Research over the past two decades has examined how landscape composition affects agroecosystem natural enemy communities and processes, and three general patterns have emerged. First, the diversity and abundance of natural enemies increases as noncrop habitat increases in the surrounding landscape. A recent review found generalist predators and host-specific parasitoids overall respond positively to increasing complexity at landscape scales (Chaplin-Kramer et al. 2011, Bianchi et al. 2006). Second, landscapes can have strong impacts

on natural enemies' biological control ability (Thies and Tschnartke 1999), though thresholds in landscape composition may exist below which they cannot provide effective natural pest suppression (With et al. 2002). Third, landscape composition can affect natural enemy species, guilds, or trophic levels differently.

Often studies examining the relationship between landscape composition and insect natural enemies in agricultural landscapes do not consider any factors other than the landscape variables of interest. Several studies have explicitly acknowledged a lack of research that examines how both landscape and abiotic factors contribute to insect populations (Noma et al. 2010). In contrast, studies on invasive insects (Trotter et al. 2013) and insect-vector-borne epidemiology (Ruiz et al. 2010) include examples of studies incorporating both abiotic and landscape drivers of insect populations. The inclusion of both in these studies led to stronger explanatory power of population patterns. Agricultural landscape studies of insect natural enemies could benefit from adopting a similar approach. Moreover, abiotic factors may or may not be correlated with landscape composition. Including abiotic factors in models will indicate the variance in natural enemy populations due to each.

Understanding natural enemy response to changes in temperature and moisture in particular is especially critical, as drought events and heat waves are predicted to increase due to climate change. Yet the consequences for plant-insect and insect predator-prey interactions are not yet well understood (Aguilar-Fenollosa and Jacas 2014). Temperature strongly affects development rates of insects and recent research indicates potential shifts in predation due to direct effects of temperature on both crop pest and natural enemy phenology and demographics (Aguilar-Fenollosa and Jacas 2014, Logan et al. 2006). Moisture levels could alter plant-insect

interactions through a variety of pathways, including changes in the host plant and the herbivorous insect – which would have implications for higher trophic levels. Previous research indicates that reduced moisture availability can lead to increased crop pest feeding and abundance (Zhang et al. 2009, Koltunov and Andreeva 1999). This theoretically could in turn provide more resources for natural enemies feeding on those crop pests, but the direct effects of drought on the natural enemies in those studies were not clear. Further research has indicated that there might be interacting effects of reduced moisture availability and plant community composition on herbivorous insects via changes in leaf chemistry (Walter et al. 2012), which could affect generalist predators that consume crop derived resources in addition to insect prey.

In this study, we were interested in exploring the effects of landscape composition, abiotic conditions, and prey availability on insect natural enemy communities of soybean. Soybean (*Glycine max*) is a leguminous crop plant widely grown worldwide. It has one major crop pest in the Midwest US, the soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae]). Soybean aphid outbreaks are associated with reduced plant height, bean size, bean quality, and yield (Ostlie 2001). Generalist predators, especially lady beetles (*Coccinellidae*), have been shown to play a key role in suppressing soybean aphid populations in the US (Landis et al. 2004, Costamagna and Landis 2006, Costamagna et al. 2007, Costamagna et al. 2008). The two most voracious predators in soybean agroecosystems in the Midwest US are considered to be *Harmonia axyridis*, a lady beetle, and *Orius insidiosus*, a predatory true bug. While there are several parasitoids established in this region, they are not considered to have as strong an impact on crop pest suppression as generalist predators (Costmagna and Landis 2006, Kaiser et al. 2007,

Noma et al. 2010). Parasitism has been much less influential than predation during soybean aphid outbreaks (Rutledge et al. 2004).

Our specific objectives were (1) to determine the contribution of landscape composition to natural enemy abundance in the soy agroecosystem (2) to determine the contribution of temperature, drought stress, and prey availability on natural enemy abundance and community composition. Our hypotheses were that increasing proportions of soy, other types of agriculture and grasslands in the landscape will be positively correlated with natural enemy abundance, because we expect to find more abundant natural enemies in landscapes with increased proportions of other agriculture, such as corn, and grasslands, given their ability to prey switch and use crop-derived resources, as found in previous studies (Gardiner et al. 2010, Donaldson et al. 2007). We anticipated that soy as a habitat will attract natural enemies via prey aggregation (Yasuda and Ishikawa 1999). We also hypothesized that increased temperature and drought stress will be negatively correlated with natural enemy abundance. We anticipated that drought and temperature stress would reduce soybean plant health, reducing food quality for soybean crop pests, and in turn decreasing the quantity and quality of prey available for natural enemies.

## **Materials and Methods**

### *Natural enemy counts*

We collected generalist natural enemies by sweep net sampling in soybean fields across Wisconsin (Figure 1). Sweep nets were 15" in diameter and made of canvas. Sweep net sampling is considered an effective sampling method for insect natural enemies in soybean (Bannerman et al. 2015). We visited a total of 1082 commercial soybean fields between 2010 and 2014. Sweep

samples were standardized between sites by taking a 100-sweep sampling effort using back-and-forth strokes across the top of the soybean foliage no closer than 50 meters from any field edge within each field. Sweep samples were transferred to labeled plastic bags and frozen after collection for later identification in the laboratory under a stereo microscope. At the time of sampling, we recorded the growth stage soybean plants in each sampling field (Licht 2014). Each sampling site was visited between 1 and 6 times between June and September in a given year. No sampling sites were revisited for sampling in subsequent years.

We aggregated natural enemy observations from sweep samples into four taxonomic groups representing seven families: lady beetles (*Coleoptera: Coccinellidae*), predatory flies (*Diptera: Syrphidae and Dolichopodidae*), predatory true bugs (*Hemiptera: Anthocoridae, Nabidae*), and lacewings (*Neuroptera: Chrysopidae and Hemerobiidae*). Counts were  $\log_{10}(x+1)$  transformed prior to analysis to normalize residuals. Sweep samples also captured parasitic wasps (*Hymenoptera: Brachonidae, Ichneumonidae*), but they were excluded from subsequent analyses for two reasons. First, generalist predators are considered more predominant and effective biological control agents of soybean aphid prey in Wisconsin and the upper Midwest (Costmagna et al. 2007, Noma et al. 2010). Second, as many parasitic wasps are specialists, the broad level of taxonomic resolution of our dataset was less appropriate than for generalist organisms with more similar life history traits.

### *Soybean aphid counts*

At each site, we counted all the soybean aphids on 5 plants at four different stations (at the corners of a 20 x 20 m square), a minimum of 50 m from the edge of the field, for a total of 20

whole-plant counts per field. This sampling approach matches standard practices used to monitor soybean aphids by crop scouts and researchers (Ragsdale et al. 2007, Stack Whitney et al. 2016). We recorded all aphid counts and calculated the average number of soybean aphids per plant for each site. Average aphid counts were  $\log_{10}(x+1)$  transformed prior to analysis to normalize model residuals.

### *Landscape composition*

We collected geospatial data at each sampling site with GPS handheld receivers on the first visit. We determined landscape composition at each sampling site using annual satellite-derived land cover imagery for 2010 through 2014 from the National Land Cover Database and the Cropland Data Layer (MRLC, USDA NASS). We imported annual land cover maps into Arc GIS version 10 software (ESRI 2011), and a map of a 1.5 kilometer radius circle area around the GPS coordinate of the center of each sampling site was extracted. We aggregated raw land cover class output into the following categories, expressed as proportions of the landscape: soybean, corn, other agriculture, forest, grasslands, water, and developed/urban, and other. Proportions were square-root transformed before analysis to normalize residuals. Only five land cover categories were included in our analysis: soybean, corn, other agriculture, forest, and grasslands. We selected these classes and our spatial scale of interest based on previous research indicating relevance to soybean pests and their natural enemies (Woltz et al. 2012, Gardiner et al. 2009a). Aggregating landscape composition categories from the raw land cover classes was also done to increase land cover prediction accuracy, which varies widely for individual land cover classes. “Other agriculture” included all annual (not including soybean and corn) and perennial non-grassland crops, such as small grains, alfalfa, and beans. “Forest” included deciduous, evergreen,

and mixed forests. “Grassland” included both managed (e.g., pasture) and natural (e.g., restored prairie) grasslands. “

### *Temperature*

We considered the cumulative seasonal effect of temperature on natural enemy abundance using growing degree days. Growing degree days (GDD) measure heat accumulation throughout the calendar year, expressed in GDD units. We used the basic method equation, which takes the average of the daily minimum and maximum temperatures compared to a base temperature (McMaster and Wilhelm 1997). We used a base temperature of 10 °C and no high temperature cut-off, based on empirically-derived temperature thresholds for soybean in the Midwest US. For each sampling site, we calculated GDD from January 1st of the year through the sampling date. GDD was calculated for each sampling site and date using an open source calculator from University of Wisconsin Cooperative Extension (University of Wisconsin Cooperative Extension: [http://agwx.soils.wisc.edu/uwex\\_agwx/thermal\\_models/degree\\_days](http://agwx.soils.wisc.edu/uwex_agwx/thermal_models/degree_days)), which incorporates the latitude and longitude for each sampling site to the nearest tenth of a decimal degree. The calculator uses raw daily temperature measurements from the Surface Weather Observation Station (AWOS/ASOS) network across Wisconsin and interpolated the point observations into grids with 13 square kilometer pixels on a 0.4 degree pitch.

We measured moisture availability at each sampling site and date using drought scores, calculated from weekly datasets produced by the United States Drought Monitor data, based on climatic, hydrologic, and soil conditions (NDMC). We downloaded their 2010 through 2014 weekly maps, imported them into Arc GIS Version 10 (ESRI 2011), and used the sampling sites’

GPS coordinates to extract drought stress values. Drought stress values are reported as scores of D0 (Abnormally Dry) through D4 (Exceptional Drought), which correspond to Palmer Drought Index scores of -1.0 to -1.9 to -5.0 or less, respectively. We converted these scores into 0 through 5 scores, so that a score of 0 at a given sampling site represented no drought stress and 5 represented exceptional drought.

### *Statistical analysis*

To model natural enemy abundance as a function of landscape, abiotic factors, and prey density, we used generalized additive models (GAMs), using the *mgcv* package in R (Wood 2011). The advantages of using GAMs are that they do not assume any particular relationship between the explanatory and response variables and allow non-linear effects, which allow nuanced exploration of species' responses to environmental factors without a priori assumptions (Guisan & Zimmermann 2000; Elith & Leathwick 2009). The large number of zeros in our data prevented using modeling approaches that require common distributions, even with common data transformations. As such, we used a two stage approach. The first stage was to use GAMs for presence-absence analysis using binomial logistic regression and restricted maximum likelihood estimation. The second stage was to use GAMs for abundance-only analysis using multiple regression with gamma distributions and restricted maximum likelihood estimation.

Our fixed effects were landscape variables (proportions of soybean, corn, other crops, grassland, and forest), abiotic variables (GDD, drought stress), and soybean aphid abundance. As random effects in the GAMs, we included year, soybean growth stage, and a spatial correlation term using latitude and longitude. Soybean growth stage was included to account for spatial and

temporal variation in the progression of the growing season across the study area and between years. The spatial term was included to account for potential spatial autocorrelation between measurements and to improve the model fit by accounting for variability not accounted for in the fixed effects. Therefore, fixed effects can be interpreted as the unique partial contributions of each factor independent of other factors, while accounting for other unexplained spatial structure in the data. We assessed model fits using reported adjusted- $R^2$  values and deviance explained scores.

The spatial correlation structure of our dataset necessitated only including one observation for each sampling location with this modeling approach. Fields were not sampled again across years, but some fields were sampled between 2 and 6 times within one year. For fields with multiple natural enemy counts within a sampling year, we took a random stratified subsample of our dataset, by randomly selecting one observation per study site (n=655).

## **Results**

### *Natural enemy counts*

We collected 1082 sweep samples of soybean natural enemies at 655 unique sites between 2010 and 2014 (Appendix 1). We collected a diverse natural enemy community in the soybean fields we sampled across Wisconsin between 2010 and 2014 (Appendix 2). Our collections included the most important predators of soybean pests in the Midwest US, lady beetle *Harmonia axyridis* and predatory true bug *Orius insidiosus*, as well as many others. All the organisms found in our survey are listed as known biological control agents of soybean aphid in the US (Ragsdale et al. 2011). Analyzing our presence and abundance models using all generalist predator natural

enemies together was not highly informative (Appendix 3). Total predator presence was significantly associated only with soybean aphid abundance (Appendix 3, adjusted  $R^2=0.086$ , deviance explained=15%), and total predator abundance was significantly associated with every fixed effect tested (Appendix 3, adjusted  $R^2=0.244$ , deviance explained= 35.8%).

### *Lady beetles*

Modeling lady beetle occurrence using presence-absence GAMs showed that lady beetle presence was positively correlated with increasing proportions of corn in the landscape (Figure 1C) and soybean aphid abundance (Figure 2B), using a cutoff of  $p<0.05$  (Appendix 4, adj- $R^2=0.217$ , deviance explained=20.2%).

273 of our 655 randomly selected site-observations had lady beetles present; these observations were included in our abundance-only GAM (Appendix 4, adj- $R^2=0.487$ , deviance explained=52.4%). Lady beetle abundance was slightly negatively correlated with corn (Figure 3A) and grassland (Figure 3D) in the surrounding landscape. Lady beetle abundance was not linearly correlated with either forest or other crops in the landscape, yet lady beetle abundance was observed to be higher where more forest or other crops were higher (Figure 3E, Figure 3C). Lady beetle abundance was also positively correlated with drought stress (Appendix 4) and with increasing soybean aphid abundance (Figure 4C).

### *Predatory flies*

Modeling predatory fly occurrence using presence-absence GAMs showed that predatory fly presence had a bimodal response to increasing soybean aphid abundance (Figure 2E, Appendix

5), using a cutoff of  $p < 0.05$  ( $\text{adj-R}^2 = 0.225$ , deviance explained = 23.1%). Predatory fly occurrence was negatively correlated with drought stress (Figure 2B).

216 of our 655 randomly selected site-observations had predatory flies present; these observations were included in our abundance-only GAM (Appendix 5,  $\text{adj-R}^2 = 0.223$ , deviance explained = 43.3%). Predatory fly abundance exhibited an overall negative correlation with increasing proportions of grassland (Figure 3D) and an overall positive correlation with forest in the landscape (Figure 3E). Predatory fly abundance showed a bimodal curve relationship with growing degree days (Figure 4A), and a unimodal response to increasing soybean aphid abundance (Figure 4C).

#### *Predatory true bugs*

Modeling predatory bug occurrence using presence-absence GAMs showed that predatory bug occurrence had a unimodal response to increasing soybean aphid abundance (Figure 2D, Appendix 6), using a cutoff of  $p < 0.05$  ( $\text{adj-R}^2 = 0.116$ , deviance explained = 13.4%). A unimodal response of predatory bug occurrence was also observed to growing degree days (Figure 2A). Predatory bug occurrence had significant but nonlinear associations with drought stress (Figure 2B), as well as increasing proportions of forest in the landscape (Figure 1E).

Of our 655 randomly selected sites, 536 included observations of predatory true bugs and were included in our abundance-only GAM (Appendix 5,  $\text{adj-R}^2 = 0.192$ , deviance explained = 33.8%). Overall, predatory bug abundance responded positively to increasing proportions of corn, soy, other crops, forest, and grassland in the surrounding landscape (Figures 3A-3E). Predatory bug abundance had a unimodal response to growing degree days (Figure 4A), was positively

correlated with drought stress (Figure 4B), and exhibited a bimodal response to increasing soybean aphid abundance (Figure 4C).

### *Lacewings*

Modeling lacewing occurrence using presence-absence GAMs showed that lacewing occurrence was negatively correlated with corn in the landscape (Figure 1A), using a cutoff of  $p < 0.05$  (Appendix 7,  $\text{adj-R}^2 = 0.089$ , deviance explained = 10.6%). Lacewing occurrence was positively correlated with drought stress (Figure 2B).

Of our 655 randomly selected sites, 114 included lacewings, thus these observations were included in our abundance-only GAM (Appendix 7,  $\text{adj-R}^2 = 0.196$ , deviance explained = 30.7%).

Lacewing abundance was slightly positively correlated with soybean (Figure 4B), other crops (Figure 4C), and forest (Figure 4E) in the surrounding landscape.

## **Discussion**

Landscape associations with insect natural enemies have been widely studied, but without the inclusion of other variables, such as abiotic conditions and prey availability, known from other research to have effects on their populations. Using a large sweep sample dataset of generalist predators collected in soybean fields and a two-stage GAM analysis, we found that a combination of landscape composition, temperature as measured by growing degree accumulation, moisture availability as measured by drought stress scores, and prey availability was associated with generalist predator presence and abundance in soybean fields.

Our explicit inclusion of non-landscape potential covariates or alternate drivers gave us more confidence in the landscape associations that we did find.

### *Predator occurrence and predator abundance*

Abiotic factors were more often significant correlates of predator occurrence than of predator abundance. Across multiple taxa and total generalist predator observations, we found soybean aphid abundance to be overall positively correlated with predator occurrence. We expect this is due to predators tracking prey across the landscape, arriving to study sites when soybean aphid densities are high enough to be detected using soybean aphid alarm pheromones (Hatano et al. 2008, Verheggen et al. 2009). Predatory bugs and lacewing occurrence also responded positively to drought stress, while predatory flies had a significant negative response.

Predator occurrence responses to landscape did not directly correlate with predator abundance responses to the same landscape variables. This could indicate that different habitats influence the arrival of predators, rather than support population growth. Only predatory bugs were observed to have consistent significant matching results between occurrence and abundance models.

### *Landscape factors*

Overall, we found mixed support for our hypothesis that agricultural land cover and grassland would be positively correlated with more natural enemies in the soybean agroecosystem. In line with our first hypothesis, we did find increased proportions of other crops (non-corn, non-soy agriculture) in the landscape associated with increased occurrences of predatory flies, predatory bugs, and lacewings. We also found that increased proportions of other crops (non-corn and non-soybean agriculture) in the surrounding landscape to be positively correlated with the abundance of lady beetles, predatory bugs, lacewings and overall predator abundance. Other crops, which

can include wheat and other small grains, could be source habitats for predators that are coming to prey on soybean aphids in our sampled soybean fields (Gardiner et al. 2009b; Woltz et al. 2012). We also found predator abundance to be positively correlated with increased proportions of soy in the landscape. Soybean acreage other than our sampling sites would also provide soybean aphid prey resources for predators, and generalist predators are known to move through agricultural landscapes tracking available prey resources throughout the growing season (Elliott et al. 2002).

Additionally, we found positive correlations between lacewing and predatory fly abundance and forest acreage in the surrounding landscape. Additional and alternate prey resources could also be in forests, as noncrop habitat including forests have been found positively correlated with the abundance of other aphid species (Plecas et al. 2014) and biological control of other insect prey (Werling et al. 2011). However, contrary to our hypothesis, we found increased proportions of corn in the surrounding landscape to be negatively correlated with predator occurrence and abundance. This finding is also contrary to previous research in the same system (e.g. Stack Whitney et al., Chapter 3) which found both that overall predator abundance most strongly associated with increased proportions of corn in the surrounding landscape and that increasing proportions of corn were also strongly associated with soybean aphid suppression, under experimental conditions. Similarly, contrary to our hypothesis, we found grassland in the surrounding landscape to be negatively correlated with lady beetle abundance, but positively correlated with predatory bug abundance. This finding is also contrary to previous research that found lady beetles associated with higher proportions of grassland in the landscape (Gardiner et al. 2009b). The heterogeneous responses we observed by soybean natural enemies to habitats, in

contrast to the consistently strong response of predator occurrence to soybean aphid densities, could indicate that natural enemies are responding to prey availability, for which land cover may not always be an appropriate proxy measurement.

One reason our findings may differ from previous results because we included a spatial correlation term in our models, while previous studies in this system in this region have not. As a consequence, our analysis approach allowed for nonlinear relationships, and this could be evidence of the consequence of including abiotic conditions and prey availability as potential drivers of our response variable, in addition to landscape composition. Furthermore, the large spatial extent of our data and large sample size across 5 years might reveal different patterns than studies done within 1 growing season or with fewer sites in a small region.

#### *Abiotic factors*

Contrary to our second hypothesis, we did not see a negative response across the board to increased growing degree days by most taxa. We observed that generalist predator occurrence and abundance overall exhibited unimodal responses to growing degree days. This potentially indicates a threshold past which up until crossing it is beneficial for soybean predators, but then past that additional degree day accumulation is not. Stronger effects of climate change are predicted for higher trophic levels due to bottom up amplification (Voigt et al. 2003, Cagnolo et al. 2002), but generalist predators may be less at risk because of their ability to switch prey.

Similarly, we also did not find strong negative responses to reduced moisture availability as measured by drought stress scores. While we found some evidence that predator occurrence was

negatively associated with increased drought scores, lady beetle, predatory bug, and overall predator abundance were slightly positively correlated with drought scores. This result was surprising, given that our study included a period of severe drought across Wisconsin in 2012. Reduced moisture has been found to lead to increased insect pest abundance and feeding (Koltunov and Andreeva 1999). Increased drought stress could aid natural enemy orientation by supporting prey aggregation, allowing aphidophagous predators to navigate toward plant volatiles emitted in response to this increased herbivory (Sasso et al. 2009). Another possible explanation is that soybean is a relatively drought tolerant crop, more so than other commodity crops, and has been selectively bred to better tolerate drought. Growers may be selecting soybean varieties that are well suited to their local climate and soil conditions, resulting in plants that don't easily exhibit stress or can tolerate some periods of reduced moisture.

Our findings about abiotic conditions and generalist predator communities in soybean may differ from our hypotheses because of how we measured temperature and moisture. Cumulative growing degree days are a standard measurement for seasonal temperature patterns in agronomy and entomology research. However, a field can accumulate the same number of growing degree days by very different shaped curves that may or may not include extreme, acute weather events. Using cumulative growing degree days masks variation within season between sites, and it's possible that the timing or frequency of acute weather events contributes more to variation of natural enemy presence and abundance than our cumulative metric could capture. Furthermore, other abiotic conditions also change during the growing season as growing degree days accumulate. There are potentially confounding factors, such as photoperiod or plant nutrient status, that are not included in our analyses.

Conversely, using drought stress scores as a measure of moisture availability may be well suited to our instantaneous sweep measure of natural enemy communities, but does not provide seasonal context. Weekly drought scores alone cannot reveal how long a field has been experiencing continuous stress or reveal the timing of acute extreme events that may have occurred previously in a field. It's possible that the timing or frequency of heavy rainfall events or extreme dry conditions would reveal different associations with predator and prey abundances in the soy agroecosystem.

#### *Prey abundance*

We found prey availability, as measured by soybean aphid abundance, to be an important model component in our analyses of most taxa observed. However, natural enemy responses to increasing soybean aphid abundance had large confidence intervals at the highest aphid densities. Looking at the patterns with the most frequent soybean aphid densities, overall generalist predators responded positively to soybean aphid abundance. This finding is in line with previous research on soybean generalist predators. For example, coccinellids are strongly influenced by the presence of soybean crop pests (Koh et al. 2013). In general, we expected predators to respond to and navigate towards honeydew odors or soybean aphid alarm pheromones (Hatano et al. 2008, Verheggen et al. 2009). Our finding of strong but nonlinear relationships with prey availability could indicate that predators are indeed responding to soybean aphid aggregations.

#### *Conclusions*

Using a large dataset composed of one-time observations for this study presented many opportunities. We were able to include many factors in our models to test as competing drivers of natural enemy presence and abundance. Yet while we were able to explain some of the variation in abundance, the R-squared and deviance explained for our models was not above 50%. This could be because our taxonomic groupings were too coarse, introducing too much noise to see stronger patterns. The taxonomic groupings may mask the responses of particular species to different habitats in the surrounding landscape, and depending on which species dominate the assemblages, contrasting results from previous studies could be obtained. Alternatively, we may not have had enough variation in the response variables. Sweep-net sampling using 100-sweep count sampling efforts may not yield enough variation between sites to pick up patterns. The inclusion of certain taxa themselves could also be problematic, as syrphids and chrysophids, which were often collected in our survey as adults, do not eat soybean aphids as adults; yet we included them because they are important beneficial insects whose larval stages eat aphids in soybean fields. Lastly, our findings about generalist predators are limited by the geographic and temporal scope of our study. While there are importation implications for how crop natural enemies could respond in future or no-analog conditions, these findings should not be used to predict insect populations in specific fields.

Our results broadly support the inclusion of abiotic factors and biotic interactions in models of natural enemy community abundance and diversity. Our analysis of natural enemy community data from soybean fields in the Midwest US suggests that changes in landscape composition do affect soybean natural enemy community composition and abundance. Unlike previous studies and theory expecting only noncrop habitat to support increased abundance and diversity of

natural enemies, we found both crop and noncrop habit to influence natural enemy presence. Overall predator abundance was positively correlated with both crop and noncrop habitat in the surrounding landscape. However, the specific habitats and direction of those relationships depends on the taxonomic group of interest – as well as other non-landscape drivers tested including temperature, drought stress, and prey availability. The consistent signal of prey availability observed, combined with the heterogeneous response of natural enemies to habitat types, indicates the importance of explicitly testing resource availability, rather than simply land use categories. Future research on natural enemies in agricultural landscapes should include these and other non-landscape factors, to increase understanding of how climate change impacts may alter previously understood relationships between natural enemies, their prey, and crop plants.

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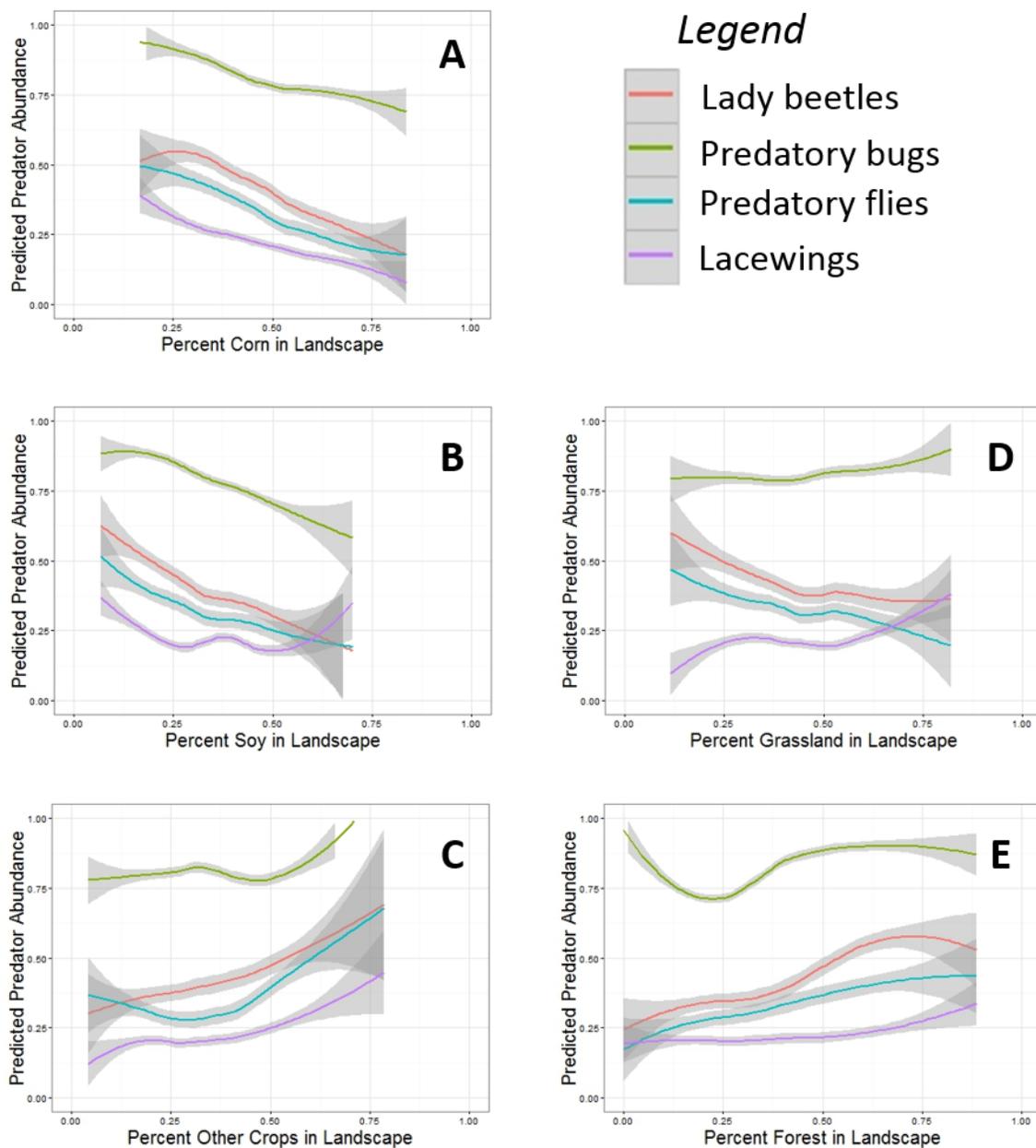
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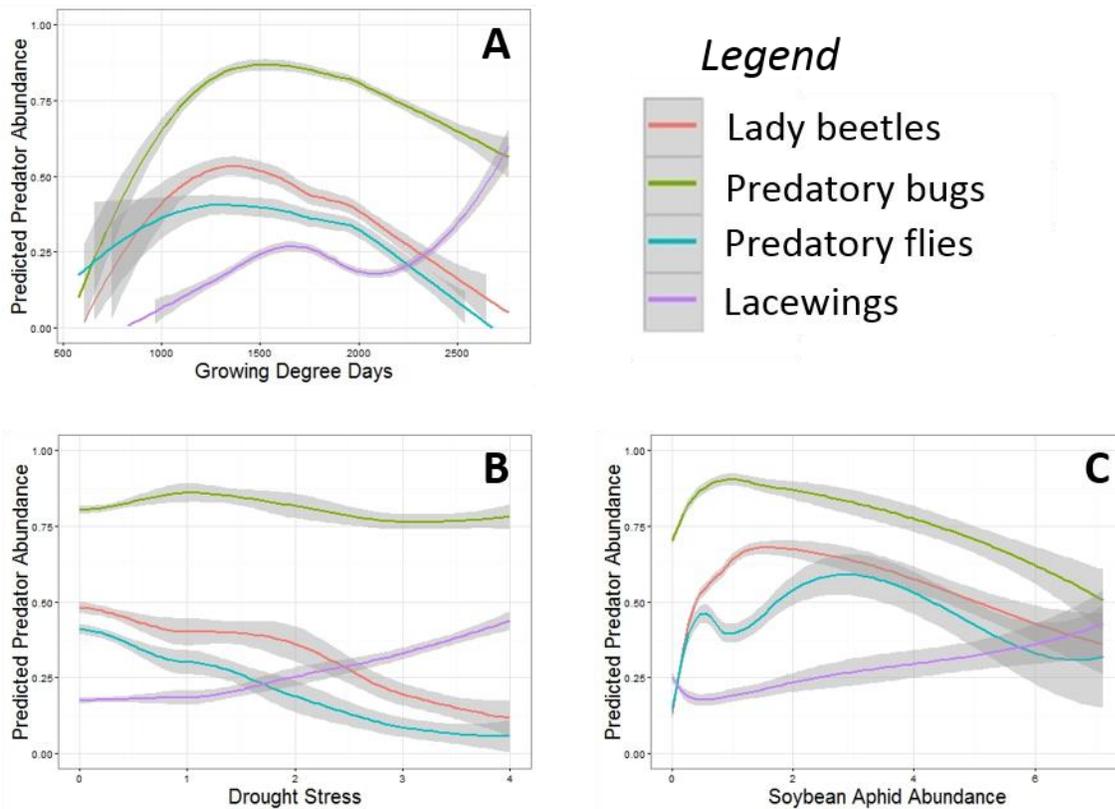
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## Figures

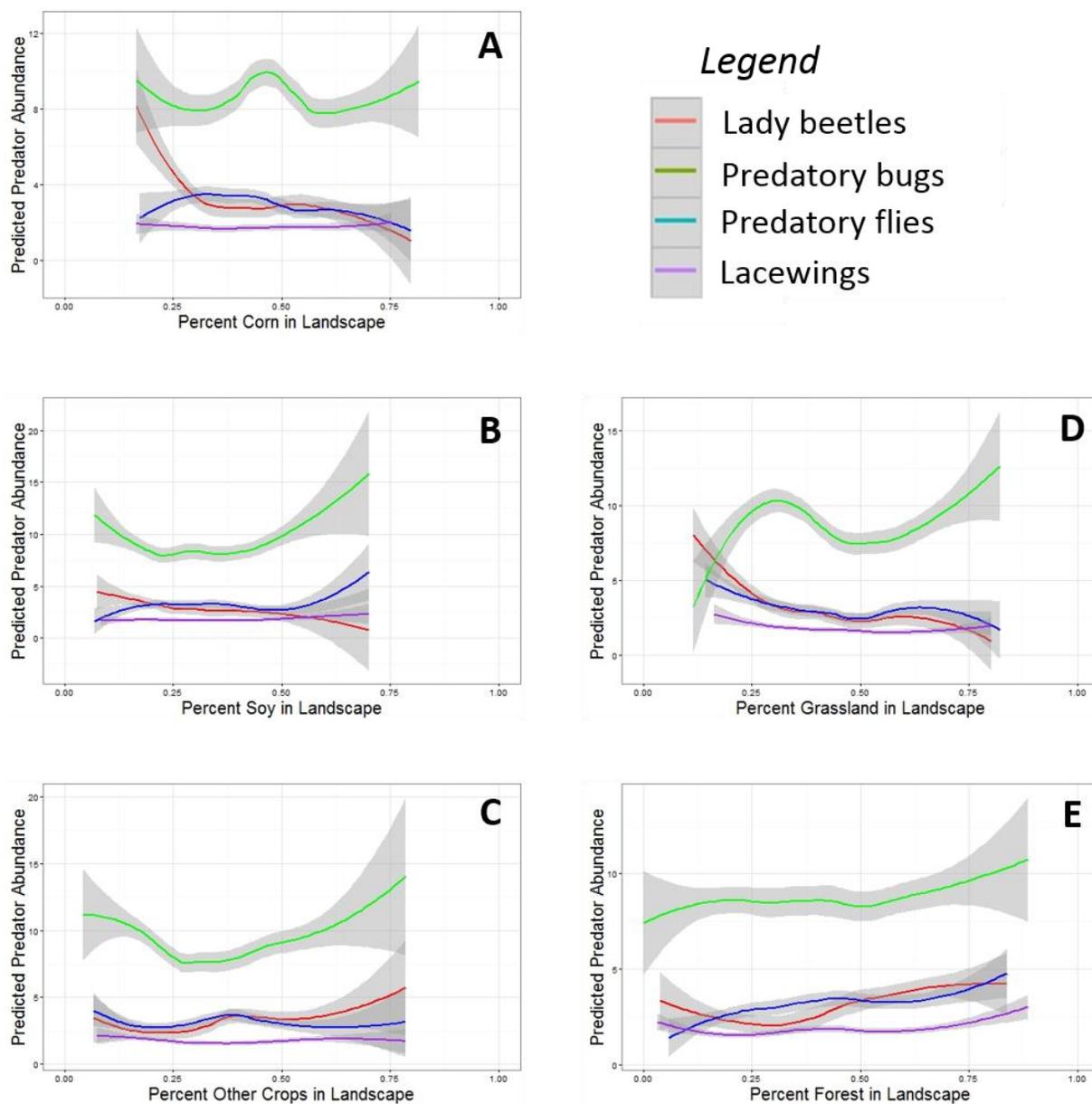


**Figure 1A-1E.** Results of the presence/absence generalized additive model (GAM) predicted occurrence of lady beetles, predatory flies, predatory bugs, and lacewings versus landscape composition features (square-root transformed). Colored lines, each representing one of the four generalist predator functional groups collected, show smoothed trend lines of all data points with

gray bars representing the 95% confidence interval. **Figure 1A.** Predator presence was overall negatively correlated with increasing proportions of corn in the surrounding landscape. **Figure 1B.** Predator presence was overall negatively correlated with increasing proportions of soy in the surrounding landscape. **Figure 1C.** Predator presence was overall positively correlated with other crops (non-corn, non-soy agriculture) in surrounding landscape. **Figure 1D.** Predatory bugs and lacewings were positively correlated with grassland in the surrounding landscape, while lady beetle and predatory fly occurrence was negatively correlated with grassland. **Figure 1E.** Predator presence was overall positively correlated with increasing proportions of forest in the surrounding landscape.

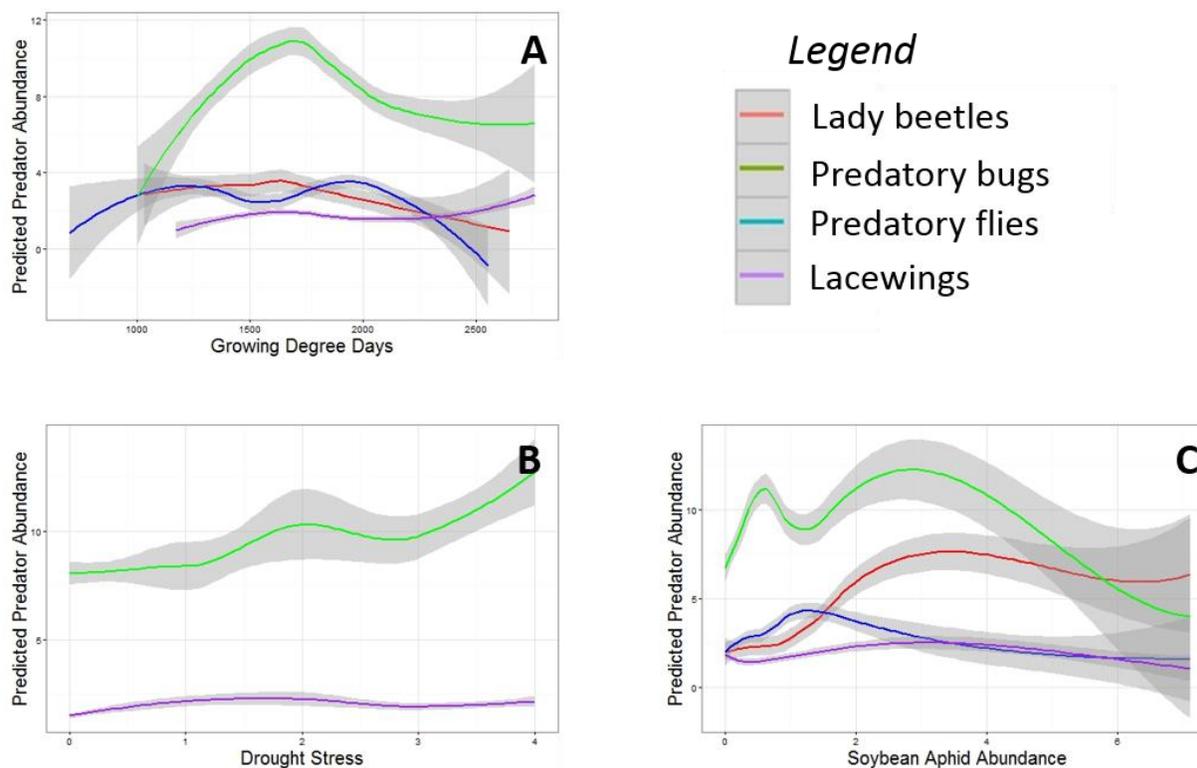


**Figure 2A-2C.** Results of the presence/absence generalized additive model (GAM) predicted occurrence of lady beetles, predatory flies, predatory bugs, and lacewings versus landscape composition features (square-root transformed). Colored lines, each representing one of the four generalist predator functional groups collected, show smoothed trend lines of all data points with gray bars representing the 95% confidence interval. **Figure 2A.** Predator presence overall had a unimodal response to increasing growing degree day accumulation. **Figure 2B.** Lacewing presence was positively correlated with increased drought stress, while lady beetle and predatory fly occurrence was not. **Figure 2C.** Predator presence had nonlinear responses to increasing soybean aphid abundance. Overall pattern for lady beetle and predatory bug occurrence was unimodal, while predatory fly response was bimodal.



**Figure 3A-3E.** Results of the abundance-only generalized additive models (GAM) predicted occurrence of lady beetles, predatory flies, predatory bugs, and lacewings versus landscape composition features (square-root transformed). Colored lines, each representing one of the four generalist predator functional groups collected, show smoothed trend lines of all data points with gray bars representing the 95% confidence interval. **Figure 3A.** Predator abundance was not

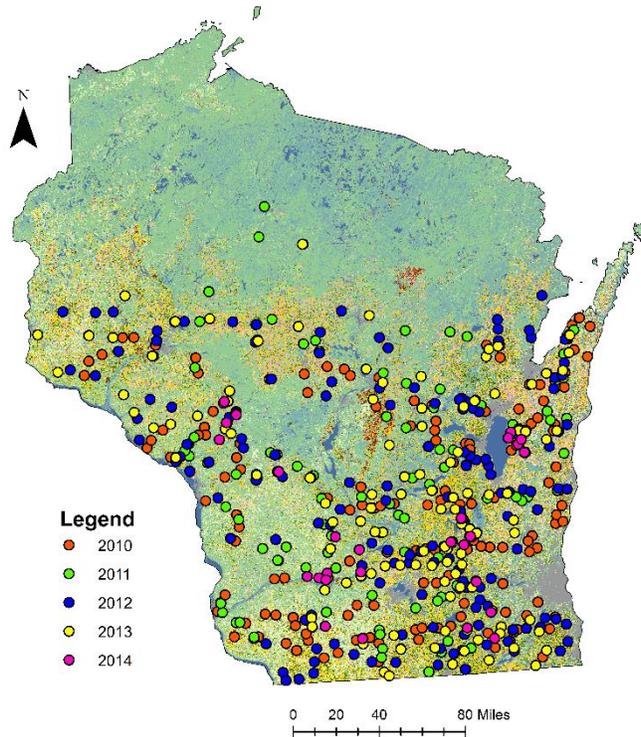
linearly correlated with increasing corn in the landscape. **Figure 3B.** Predator abundance was not linearly correlated with increasing soy in the landscape. **Figure 3C.** Predator abundance overall did not exhibit a positive or negative correlation with increasing other crops (non-corn, non-soy agriculture) in the surrounding landscape. **Figure 3D.** Lady beetle and predatory fly abundance were negatively correlated with increasing grassland in the landscape, while predatory bug abundance was overall positively correlated with grassland. **Figure 3E.** Predator abundance was overall positively correlated with increasing proportions of forest in the landscape.



**Figure 4A-4C.** Results of the abundance-only generalized additive models (GAM) predicted occurrence of lady beetles, predatory flies, predatory bugs, and lacewings versus landscape composition features (square-root transformed). Colored lines, each representing one of the four generalist predator functional groups collected, show smoothed trend lines of all data points with gray bars representing the 95% confidence interval. **Figure 4A.** Lady beetle and predatory bug abundance had a unimodal response to increasing growing degree day accumulation, while predatory fly abundance exhibited a bimodal response. **Figure 4B.** Predatory bug abundance was positively correlated with drought stress. Lady beetle and predatory fly models did not successfully converge. **Figure 4C.** Predatory bug abundance had bimodal response to increasing soybean aphid abundance, while abundance of lady beetles, predatory flies, and lacewings had smaller unimodal correlations.

## Supplemental Appendices

### Appendix 1.



Locations of our natural enemy collections via sweep net sampling in commercial soybean fields across Wisconsin between 2010 and 2014.

## Appendix 2.

### Soy natural enemy insects collected and identified in this study

#### **Lady beetles:** (Family Coccinellidae, Order Coleoptera)

*Adalia bipunctata* (2-spotted / orange spotted)

*Coccinella novemnotata* (9-spotted)

*Coccinella septempunctata* (7-spotted / C-7)

*Coccinella trifasciata* (3-banded)

*Coleomegilla maculate* (Pink spotted / 12-spotted)

*Harmonia axyridis* (Asian multi-colored)

*Hippodamia convergens* (Convergent)

*Hippodamia parenthesis* (Parenthesis)

*Hippodamia tredecimpunctata* (13-spotted)

*Hippodamia variegata* (Variegated)

*Psyllobora vigintimaculata* (20-spotted)

Other larva (not identified further than Coccinellidae)

#### **Predatory flies:** (Order Diptera)

Dolichopodidae (Long legged flies)

Syrphidae (Hover flies)

#### **Predatory true bugs:** (Order Hemiptera)

Anthocoridae, *Orius insidiosus* (Minute pirate bug)

Lygaeidae (Big-eyed bug)

Nabidae (Damsel bug)

Reduviidae (Assassin bug)

#### **Lacewings:** (Order Neuroptera)

Chrysopidae (Green lacewings)

Hemerobiidae (Brown lacewings)

Larva (not identified further than Neuroptera)

## Appendix 3.

## Total generalist predators

Predictor variable	<i>Presence/Absence Model</i> (adjusted R <sup>2</sup> =0.086, deviance explained=15%)				<i>Abundance Model</i> (adjusted R <sup>2</sup> =0.244, deviance explained= 35.8%)			
	edf	Ref.df	Chi. sq	p-value	edf	Ref.df	Chi. sq	p-value
<i>Fixed effect</i>								
<b>Corn</b>	3.710	4.647	6.841	---	<b>8.756</b>	<b>8.981</b>	<b>90.151</b>	<b>***</b>
<b>Soy</b>	1.000	1.000	2.781	---	<b>8.757</b>	<b>8.980</b>	<b>65.196</b>	<b>***</b>
<b>Other crops</b>	1.000	1.000	0.012	---	<b>6.666</b>	<b>7.745</b>	<b>110.553</b>	<b>***</b>
<b>Grassland</b>	1.658	2.084	1.214	---	<b>8.839</b>	<b>8.991</b>	<b>141.303</b>	<b>***</b>
<b>Forest</b>	1.000	1.000	0.160	---	<b>8.555</b>	<b>8.943</b>	<b>90.378</b>	<b>***</b>
<b>Growing Degree Days</b>	1.525	1.885	1.360	---	<b>6.139</b>	<b>7.187</b>	<b>168.920</b>	<b>***</b>
<b>Soybean aphid abundance</b>	<b>3.137</b>	<b>3.825</b>	<b>13.125</b>	<b>**</b>	<b>8.998</b>	<b>9.000</b>	<b>709.697</b>	<b>***</b>
<b>Drought</b>	1.499	1.738	1.104	---	<b>1.980</b>	<b>1.999</b>	<b>356.245</b>	<b>***</b>
<i>Random effect</i>								
<b>Year</b>	<0.000	1.000	0.000	---	<b>&lt;0.000</b>	<b>1.000</b>	<b>0.000</b>	<b>***</b>
<b>Growth stage</b>	3.057	21.000	5.479	---	<b>17.12</b>	<b>19.000</b>	<b>222.178</b>	<b>***</b>
<b>Latitude ~ Longitude</b>	0.7404	1.000	1.495	---	0.535	1.000	2.222	---

\* p&lt;0.05 \*\* p&lt;0.01 \*\*\*p&lt;0.001

## Appendix 4.

## Lady beetles

Predictor variable	<i>Presence/Absence Model</i> (adjusted R <sup>2</sup> =0.217, deviance explained=20.2%)				<i>Abundance Model</i> (adjusted R <sup>2</sup> =0.487, deviance explained= 52.4%)			
	edf	Ref.df	Chi. sq	p-value	edf	Ref.df	Chi. sq	p-value
<i>Fixed effect</i>								
Corn	1.000	1.000	0.421	---	<b>4.281</b>	<b>5.280</b>	<b>17.289</b>	<b>**</b>
Soy	1.000	1.000	0.087	---	6.186	7.283	10.869	---
Other crops	<b>1.000</b>	<b>1.000</b>	<b>4.468</b>	<b>*</b>	<b>6.507</b>	<b>7.556</b>	<b>31.244</b>	<b>***</b>
Grassland	1.383	1.676	0.699	---	<b>2.345</b>	<b>2.927</b>	<b>9.724</b>	<b>*</b>
Forest	3.036	3.793	5.141	---	<b>8.537</b>	<b>8.922</b>	<b>25.210</b>	<b>**</b>
Growing Degree Days	1.951	2.481	4.554	---	7.410	8.373	15.408	---
Soybean aphid abundance	<b>8.269</b>	<b>8.834</b>	<b>64.170</b>	<b>***</b>	<b>6.576</b>	<b>7.444</b>	<b>79.398</b>	<b>***</b>
Drought	1.562	1.801	3.138	---	<b>1.002</b>	<b>1.003</b>	<b>8.022</b>	<b>**</b>
<i>Random effect</i>								
Year	<0.000	1.000	0.000	---	<0.000	1.000	0.000	---
Growth stage	3.806	21.000	12.628	<b>**</b>	<b>10.540</b>	<b>15.000</b>	<b>23.239</b>	<b>**</b>
Latitude ~ Longitude	<0.000	1.000	0.000	---	0.928	1.000	3.684	---

\* p<0.05 \*\* p<0.01 \*\*\*p<0.001

## Appendix 5.

## Predatory flies

Predictor variable	<i>Presence/Absence Model</i> (adjusted R <sup>2</sup> =0.225, deviance explained=23.1%)				<i>Abundance Model</i> (adjusted R <sup>2</sup> =0.223, deviance explained= 43.3%)			
	edf	Ref.df	Chi. sq	p-value	edf	Ref.df	Chi. sq	p-value
<i>Fixed effect</i>								
Corn	1.000	1.000	2.478	---	7.012	8.065	15.584	---
Soy	1.000	1.000	0.368	---	2.965	3.631	7.515	---
Other crops	3.985	4.967	5.787	---	1.643	2.068	1.415	---
Grassland	1.000	1.000	0.607	---	<b>8.791</b>	<b>8.978</b>	<b>26.097</b>	<b>**</b>
Forest	1.000	1.000	0.292	---	<b>4.404</b>	<b>5.355</b>	<b>20.628</b>	<b>**</b>
Growing Degree Days	1.753	2.218	0.987	---	<b>8.200</b>	<b>8.810</b>	<b>44.255</b>	<b>***</b>
Soybean aphid abundance	<b>6.924</b>	<b>7.932</b>	<b>34.672</b>	<b>***</b>	<b>7.986</b>	<b>8.677</b>	<b>43.341</b>	<b>***</b>
Drought	<b>1.000</b>	<b>1.000</b>	<b>6.702</b>	<b>**</b>	1.002	1.004	1.220	---
<i>Random effect</i>								
Year	<0.000	1.000	0.000	---	<0.000	1.000	0.000	---
Growth stage	<b>13.420</b>	<b>21.000</b>	<b>45.098</b>	<b>***</b>	<b>0.892</b>	<b>13.000</b>	<b>16.401</b>	<b>***</b>
Latitude ~ Longitude	<0.000	1.000	0.000	---	<b>0.892</b>	<b>1.000</b>	<b>6.623</b>	<b>**</b>

\* p<0.05 \*\* p<0.01 \*\*\*p<0.001

## Appendix 6.

## Predatory bugs

Predictor variable	<i>Presence/Absence Model</i> (adjusted R <sup>2</sup> =0.116, deviance explained=13.4%)				<i>Abundance Model</i> (adjusted R <sup>2</sup> =0.192, deviance explained= 33.8%)			
	edf	Ref.df	Chi. sq	p-value	edf	Ref.df	Chi. sq	p-value
<i>Fixed effect</i>								
<b>Corn</b>	2.820	3.570	2.694	---	<b>8.889</b>	<b>8.995</b>	<b>125.901</b>	<b>***</b>
<b>Soy</b>	1.000	1.000	0.547	---	<b>6.838</b>	<b>7.924</b>	<b>57.558</b>	<b>***</b>
<b>Other crops</b>	3.165	3.986	3.636	---	<b>7.494</b>	<b>8.411</b>	<b>87.660</b>	<b>***</b>
<b>Grassland</b>	1.000	1.000	2.718	---	<b>8.871</b>	<b>8.994</b>	<b>154.404</b>	<b>***</b>
<b>Forest</b>	<b>1.000</b>	<b>1.001</b>	<b>3.990</b>	<b>*</b>	<b>8.570</b>	<b>8.947</b>	<b>96.511</b>	<b>***</b>
<b>Growing Degree Days</b>	<b>2.979</b>	<b>3.763</b>	<b>13.434</b>	<b>**</b>	<b>8.571</b>	<b>8.945</b>	<b>138.607</b>	<b>***</b>
<b>Soybean aphid abundance</b>	<b>4.737</b>	<b>5.713</b>	<b>19.271</b>	<b>**</b>	<b>8.995</b>	<b>9.000</b>	<b>415.018</b>	<b>***</b>
<b>Drought</b>	<b>1.415</b>	<b>1.648</b>	<b>4.455</b>	<b>*</b>	<b>1.950</b>	<b>1.996</b>	<b>309.269</b>	<b>***</b>
<i>Random effect</i>								
<b>Year</b>	<0.000	1.000	0.000	---	<b>0.000</b>	<b>1.000</b>	<b>0.000</b>	<b>***</b>
<b>Growth stage</b>	1.820	21.000	2.856	---	<b>111.765</b>	<b>16.000</b>	<b>111.765</b>	<b>***</b>
<b>Latitude ~ Longitude</b>	0.0716	1.000	2.225	---	3.576	1.000	3.576	---

\* p&lt;0.05 \*\* p&lt;0.01 \*\*\*p&lt;0.001

## Appendix 7.

## Lacewings

Predictor variable	<i>Presence/Absence Model</i> (adjusted R <sup>2</sup> =0.089, deviance explained=10.6%)				<i>Abundance Model</i> (adjusted R <sup>2</sup> =0.196, deviance explained= 30.7%)			
	edf	Ref.df	Chi. sq	p-value	edf	Ref.df	Chi. sq	p-value
<i>Fixed effect</i>								
<b>Corn</b>	<b>1.000</b>	<b>1.000</b>	<b>9.552</b>	<b>**</b>	1.833	2.293	1.764	---
<b>Soy</b>	4.612	5.683	5.596	---	<b>1.000</b>	<b>1.000</b>	<b>4.053</b>	<b>*</b>
<b>Other crops</b>	1.494	1.856	5.299	---	<b>1.000</b>	<b>1.000</b>	<b>6.015</b>	<b>*</b>
<b>Grassland</b>	1.476	1.819	1.233	---	1.581	1.955	2.187	---
<b>Forest</b>	1.000	1.000	0.616	---	<b>1.638</b>	<b>2.022</b>	<b>6.376</b>	<b>*</b>
<b>Growing Degree Days</b>	3.818	4.722	10.592	---	3.685	4.552	5.401	---
<b>Soybean aphid abundance</b>	1.000	1.000	3.139	---	2.092	2.554	3.061	---
<b>Drought</b>	<b>1.733</b>	<b>1.927</b>	<b>20.586</b>	<b>***</b>	1.000	1.000	3.760	---
<i>Random effect</i>								
<b>Year</b>	<0.000	1.000	0.000	---	<0.000	1.000	8.526	---
<b>Growth stage</b>	<0.000	1.000	0.000	---	<0.000	10.000	0.000	---
<b>Latitude ~ Longitude</b>	<0.000	21.000	0.000	---	<b>0.930</b>	<b>1.000</b>	<b>0.000</b>	<b>**</b>

\* p&lt;0.05 \*\* p&lt;0.01 \*\*\*p&lt;0.001

### Chapter 3

#### **Aphid suppression higher in fields with increased prey abundance and reduced moisture availability in Midwest US agroecosystem**

##### **Abstract:**

Semi-natural and natural habitats in the landscape surrounding cropland have been found in previous studies to be positively correlated with increased biological control and natural enemy diversity. This is likely due to landscapes moderating the flow of resources across habitats and into agricultural fields. Abiotic factors, including temperature and moisture, are also known to be important contributors to the abundance and activity of agricultural insect populations.

Increasing temperature and reduced moisture availability can cause insect mortality. However, arthropod activity across all trophic levels increases with warmer temperatures, which could result in either improved biological control outcomes or insect pest populations escaping control.

Our objective was to determine the contribution of landscape composition and climactic factors to biological control potential in an agroecosystem. We conducted our study on the soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae]) and its generalist predators in Wisconsin using aphid counts, sweep net collections, and clip-cage biological control experimental assays. We then used linear mixed models with abiotic and landscape factors as explanatory variables and biological control index scores as our response variable.

Biological control efficacy was positively correlated with soybean aphid abundance and drought stress. Our analysis also revealed significant interactions of growing degree days with grassland and predator abundance impacting biological control efficacy. Soybean aphid control is critical for both economic and ecological reasons, as biological control is estimated to be worth \$84

million annually in the Midwest US. The results of our study extend beyond the soybean agroecosystem, as aphidophagous predators are common in agroecosystems globally and promoting conservation biological control of crop pests could be a way to support increasing global yield demands while supporting biodiversity in agroecosystems.

**Introduction:**

Landscapes affect natural enemy movement and function via cross-habitat spillover (Tscharntke et al. 2012). Patches of semi- and natural habitat near cropland, for example, has been found to be positively correlated with increased biological control (Werling et al. 2011, Bianchi et al. 2006). Thus landscape context impact on natural enemies within local habitats in turn are important for community structure, species interactions, and ecological function at large spatial and temporal scales (Thies et al. 2005). This is important to understand, as natural enemies provide critical biological control services that help stabilize agroecosystems and potentially reduce pesticide applications and costs (Naylor and Ehrlich 1997, Power 2010).

Yet recent reviews have found that few studies look at landscape influence on both natural enemy abundance and biological control (Chaplin-Kramer et al. 2011, Veres et al. 2013). In the Chaplin-Kramer et al. meta-analysis, the evidence that landscape effects translate into biological control changes is mixed. Increased natural enemy abundance and pest control in complex landscapes can be offset by increased pest colonization, resulting in no net change at a landscape scale (Thies et al. 2005, Roschewitz et al. 2005). There is also evidence that natural habitats can promote pest populations in agricultural habitats (Zhang et al. 2007). Moreover, many natural enemies can exhibit intraguild predation, which means that natural enemy abundance and community composition may be positively, negatively, or not related to actual biological control of crop pests.

Many of the studies that have found evidence of landscape effects on biological control have been conducted at very small spatial scales. For example, plot-scale studies have found coccinellids to be effective suppression of aphids (Costamagna et al. 2006, Costamagna et al.

2007) and studies done in field-cages (Gardiner et al. 2009a) and small plots in the field (Donaldson et al. 2007) have found similar results. However, these studies conducted in small experimental conditions may not reflect the dynamics occurring at field scales, due to heterogeneity in pest populations, natural enemy pest suppression efficacy, and plant response.

Abiotic factors can be also expected to moderate natural enemy abundance and biological control services in agroecosystems. Temperature and moisture are important determinants of insect activity. Insects are very sensitive to temperature variability as poikilothermic organisms (Parmesan 2007); sudden changes in temperature or habitat moisture can kill insects (Schowalter 2011). Yet hotter and drier conditions are also known to support crop pest outbreaks (Mattson and Haack 1987). Predators are expected to be more sensitive to warmer temperatures and drier conditions than herbivores, due to bottom up amplification (Voigt et al. 2003, Cagnolo et al. 2002). Previous studies have found tritrophic interactions altered under experimental conditions under both experimental temperature and moisture gradients (Jamieson et al. 2012) and ambient conditions (Parmesan et al. 2006). Yet despite the well-established connections with landscape and climatic conditions on agricultural natural enemies separately, these factors have generally not been explicitly included in studies together. In contrast, some studies outside of agricultural systems incorporate both abiotic and landscape characteristics in models of insect abundance (e.g. Ruiz et al. 2010), but do not give insight into how such understanding may influence biological control potential.

Our objective in this study was thus to determine the contribution of landscape composition and climatic factors to biological control potential in an agroecosystem. We conducted our study on soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae], hereafter SBA) and its

predators in Wisconsin. SBA is a key pest of soybean (*Glycine max*), causing yield damage directly through phloem feeding (Ragsdale et al. 2007) and indirectly through virus transmission (Mueller et al. 2010). Previous research indicates that SBA abundance has shown that this pest responds to changes in landscape composition and climatic conditions, with higher SBA abundance associated with increased summer precipitation and proportions of forest habitat (Stack Whitney et al. 2016). Predators and parasitoids of soybean aphid have been shown to be effective controls of soybean aphids in their introduced habitat (Desneux et al. 2006, Rhainds et al. 2007, Costamagna et al. 2008). Generalist predators, especially ladybird beetles, have been shown to play a key role in suppressing soybean aphid populations in the Midwest US (Landis et al. 2004, Costamagna and Landis 2006, Costamagna et al. 2007, Costamagna et al. 2008). Increased natural and semi-natural habitat, such as grassland, in the surrounding landscape has been found to be associated with higher abundance and diversity of SBA generalist predators (Gardiner et al. 2009b; Woltz et al. 2012) potentially resulting in increased biological control (Werling et al. 2011).

Given the importance of landscape composition and abiotic factors on SBA abundance and predators, we explicitly designed our study and models to include both to understand their relative contributions to soybean aphid control. Specifically, we hypothesized that (1) Increased SBA abundance would result in more biological control, as prey aggregation will attract more natural enemies (Donaldson et al. 2007, Zhu et al. 1999) (2) Increased predator abundance would result in more biological control, as more natural enemies present will eat more SBA (3) Increased proportions of grassland and corn in landscape will result in more biological control, as they provide alternate prey resources throughout the growing season for important SBA

predators (Gardiner et al. 2009b; Woltz et al. 2012) (4) Increased temperature, as measured by growing degree days, would result in higher biological control efficacy, due to increased herbivory (5) Decreased moisture availability, as measured by higher drought stress scores, would result in lower biological control efficacy, due to increased stress on plants, pests, and predators via bottom up amplification. By combining analysis of the effects of landscape composition and climatic conditions on biological control potential of SBA by in situ natural enemies, we can develop a better understanding of the relative contribution of these factors on pest suppression. Our explicit examination of multiple drivers of SBA biological control can inform a conversation about the role of conservation biological control in agroecosystems when global-scale changes are predicted in both land use and climatic conditions in the future (Rounsevell et al. 2006).

## **Methods**

### *Soybean aphid counts*

This study was conducted at 43 sites, 18 sites in 2013 and 25 sites in 2014 (Appendix Figure 1). Each site was a commercial soybean field in Wisconsin, representing a wide range of the variation of landscape composition and climatic conditions in the state. No sampling sites were repeated between years. We collected geospatial data at each site with handheld GPS receivers on the first sampling date.

At each site, we counted all the soybean aphids on 5 plants at four different stations (at the corners of a 20 x 20 meter square), a minimum of 50 meters from the edge of the field, for a total of 20 whole-plant counts per field. We recorded all aphid counts and calculated the average number of soybean aphids per plant for each site. SBA were counted weekly and average SBA counts were calculated from the SBA counts taken the weeks of clip cage assay experiments at

each site. Average SBA counts per site were natural log transformed to normalize residuals for analysis.

#### *Natural enemy counts*

We collected generalist predators of SBA at each site by sweep net sampling. Sweep samples were standardized between sites by taking a 100-sweep back-and-forth sampling effort in the soybean foliage in the same part of the field as the SBA counts. We identified known SBA generalist predator natural enemies in Wisconsin (Noma et al. 2010) from sweep samples into seven families representing four taxonomic groups: predatory beetles (Coccinellidae, Order Coleoptera), predatory flies (Syrphidae and Dolichopodidae, Order Diptera, predatory true bugs (Anthocoridae, Nabidae, Order Hemiptera), and lacewings (Chrysopidae and Hemerobiidae, Order Neuroptera). We calculated total generalist predator abundance by summing the abundance of the observations of all seven families for each sweep sample. Average total generalist predator abundance was calculated by using total sweep counts from observations from each week of clip cage assays at each site and natural log transformed for analysis to normalize model residuals.

#### *Biological control assays*

Biological control potential was measured at each site using clip-cage experimental assays. Clip-cages were constructed from clear plastic petri dishes and measured 5cm in diameter. Some were designed to be open to predators, while others were closed to predators with mesh (mesh size 0.5mm x 0.5mm, Lumite Inc., Alto, GA). At each site, we randomly selected plants in our SBA sampling area within fields and established sets of clip-cages. One 'open' clip cage was clipped to a leaf of the top trifoliolate; one 'closed' clip cage (the control) was clipped to a different leaf on the same trifoliolate. Ten adult soybean aphids, procured from the same field on the same date,

were placed on leaves within the cages using a paintbrush. In 2013, two sets of clip-cages per field were established, while in 2014 four sets were established. Fields were revisited 7 days later, and the remaining aphids in the clip-cages were counted. Measuring population growth after a 1-week interval is commonly used for SBA monitoring (Desneux et al. 2006, Costamagna et al. 2010). The aphids were reset and results were recorded each week, as well as GPS coordinates and sampling date. Assays were conducted in late July and early August, when SBA has historically been near peak abundance (Mitchell et al. 2014a). We conducted the assays two times at each site in 2013 and three times at each site in 2014.

Biocontrol control potential was calculated as a biological control index score from assay results by the equation:

$$\text{Biological control index (BCI)} = \frac{\text{SBA}_{\text{open, final}} - \text{SBA}_{\text{closed, final}}}{\text{SBA}_{\text{open, initial}} - \text{SBA}_{\text{closed, initial}}}$$

Thus, the lower the BCI score calculated per clip-cage set, the higher the biological control potential. We calculated the average BCI score across all clip-cage sets at a site each week, and at the end of each season, we calculated the average BCI score per site.

#### *Landscape composition*

Using GPS coordinates from each site, we determined landscape composition at each sampling site using satellite-derived land cover imagery from the National Land Cover Database and the Cropland Data Layer (MRLC, USDA NASS). We imported annual land cover maps into Arc GIS version 10 software (ESRI 2011), and a map of a 1.5 kilometer radius circle area around the GPS coordinate of the center of each sampling site was extracted. We aggregated raw land cover class output into the following categories, expressed as proportions of the landscape: soybean, corn, other agriculture, forest, grasslands, water, and developed/urban. “Other agriculture”

included all annual (not including soybean and corn) and perennial non-grassland crops, such as small grains, alfalfa, and beans. “Forest” included deciduous, evergreen, and mixed forests. “Grassland” included both managed (e.g., pasture) and natural (e.g., restored prairie) grasslands. “Developed/urban” included residential and industrial land uses. Only five land cover categories were included in our analysis: soybean, corn, other agriculture, forest, and grasslands. We selected these classes and spatial scale of interest based on previous research indicating relevance to soybean pests and their natural enemies (Woltz et al. 2012, Noma et al. 2010, Gardiner et al. 2009a). Aggregating landscape composition categories from the raw land cover classes was also done to increase land cover prediction accuracy, which varies widely for individual land cover classes.

#### *Abiotic conditions*

We considered the effect of temperature using cumulative growing degree days. Growing degree days (GDD) measure heat accumulation throughout the calendar year, expressed in GDD units. We used the basic method equation (McMaster and Wilhelm 1997), with a base temperature of 10 °C, based on empirically-derived temperature thresholds for soybean in the Midwest US. For each sampling site, we calculated GDD from January 1st of the year through the last sampling date. GDD was calculated for each sampling site and date using an open source calculator from University of Wisconsin Cooperative Extension (University of Wisconsin Cooperative Extension, [http://agwx.soils.wisc.edu/uwex\\_agwx/thermal\\_models/degree\\_days](http://agwx.soils.wisc.edu/uwex_agwx/thermal_models/degree_days)), which incorporates the latitude and longitude for each sampling site to the nearest tenth of a decimal degree. The calculator uses raw daily temperature measurements from the Surface Weather Observation Station (AWOS/ASOS) network across Wisconsin and interpolated the point observations into grids with 13 square kilometer pixels on a 0.4 degree pitch.

We measured moisture availability at each sampling site and date using United States Drought Monitor drought stress scores, integrative scores based on climatic, hydrologic, and soil conditions (NDMC). We downloaded their 2010 through 2014 weekly maps, imported them into Arc GIS Version 10 (ESRI 2011), and used the sampling sites' GPS coordinates to extract drought stress values. Drought stress values are reported as scores of D0 (Abnormally Dry) through D4 (Exceptional Drought), which correspond to Palmer Drought Index scores of -1.0 to -1.9 to -5.0 or less, respectively. We converted these scores into 1 through 5 scores, where a score of 1 corresponded to D0 (Abnormally Dry) and 5 corresponded to D4 (Exceptional Drought). Sites and dates with no drought were represented by scores of 0. We calculated the average drought score across the weeks of biological control assays in each field, to get one average drought score per site for analyses.

### *Statistical Analyses*

We fit two sets of linear mixed-effects models with total predator abundance and BCI scores from each site as our response variables, using R (R Development Core Team 2008). Our fixed effects were landscape variables (proportions of soy, corn, other crops, grassland, and forest), growing degree days, and average SBA abundance. In our BCI model, fixed effects also included the average total generalist predator abundance. Fixed effects were scaled using the *scale* function in R, to enable comparison of effect sizes in analysis. As random effects in the models, we included year and a spatial term using latitude and longitude, to account for potential spatial autocorrelation between measurements and to improve the model fit by accounting for variability not accounted for in the fixed effects. Therefore, fixed effects can be interpreted as the unique partial contributions of each factor, while accounting for other unexplained spatial structure in

the data. The spatial correlation structure of our models necessitated only including one observation for each sampling location, which is why within-season averages per site were calculated from weekly measurements of insect abundance, abiotic conditions, and BCI scores. Two-way interactions were tested one at a time to avoid overfitting (Berrington de Gonzalez and Cox 1997). We removed nonsignificant interaction terms from the final model, in order to examine the main effects. We calculated model fits using a pseudo  $R^2$ , determined by comparing the squared correlation of our observed data with the fitted model predictions for each data point.

## **Results**

### *Predator abundance*

SBA populations varied greatly between sites, with a mean abundance of 245.32 aphids per plant (median = 55.28, IQR = 456.78). Generalist predator abundance was much less varied and much lower, with a mean of 4.64 predators per sweep sample (median = 4, IQR = 4.03). Using our linear mixed model, we found generalist predator abundance most strongly positively associated with increasing proportions of corn in the surrounding landscape ( $p < 0.01$ ) (Table 1, Figure 1A). Predator abundance was also positively correlated with increasing proportions of other agriculture ( $p < 0.05$ ), forest ( $p < 0.05$ ), and grassland ( $p < 0.05$ ) (Table 1, Figure 1A). We did not find any significant associations of GDD, drought stress, or SBA population density with predator abundance. No two-way interactions tested were significant. The model had a pseudo- $R^2$  of 0.56.

### *Biological control efficacy*

Our biological control experiment and subsequent analysis suggest that biological control potential was highly positively correlated with SBA abundance ( $p < 0.01$ ) (Table 1, Figure 1B).

Biological control potential was also positively correlated with increased drought stress ( $p < 0.05$ ) (Table 1, Figure 1B). The model had a pseudo- $R^2$  of 0.57.

We did not find significant associations of BCI scores with predator abundance, landscape habitats, or growing degree days. However, our analysis revealed that BCI scores were significantly influenced by two sets of interacting fixed effects (Table 1, Figures 2A-2B). Since the main effects tested were not significant, this is evidence of a crossover effect – wherein the effect of growing degree days on biological control efficacy scores depends on the proportion of grassland in the surrounding landscape and predator abundance. The positive interaction between GDD and grassland means that as GDD increases, the effect of grassland on biological control potential increases ( $p < 0.05$ ) (Figure 2B). Conversely, the negative interaction of GDD and predator abundance means that as GDD increases, the effect of natural enemy abundance on biological control potential decreases ( $p < 0.01$ ) (Figure 2A).

## **Discussion**

### *Landscape composition*

Our finding that SBA predators are positively correlated with some agricultural habitats, including corn and small grains, is evidence that agriculture can be a source of predators to agroecosystems, by providing resource pulses throughout the growing season. The exotic multicolored Asian lady beetle (*Harmonia axyridis*) and the native minute pirate bug (*Orius insidiosus*) have consistently been the most abundant predators of soybean aphid found in US soybean fields in the past decade (Costamagna et al. 2007, Gardiner et al. 2009a, Gardiner et al. 2009b). In the Midwest US specifically, ladybeetles (Coccinellidae) and predatory bugs, specifically *Orius insidiosus*, are considered the most important controls of soybean aphids (Desneux et al. 2006, Costamagna et al. 2007, Costamagna et al. 2008, Lundgren et al. 2013).

While our biological control assays did not track individual predators feeding on SBA, ladybeetles and predatory bugs were consistently collected in our sweep catches. Our study results are in line with previous studies on these organisms, which found that *O. insidiosus* populations were associated with increased landscape diversity (Seagraves and Lundgren 2010) and ladybeetles associated with higher proportions of forest and grasslands (Gardiner et al. 2009b).

Yet despite this support in our analyses for the influence of landscape composition on natural enemy abundance, our results do not support our hypothesis that landscape composition influences biological control outcomes. However, our results show the importance of explicitly including both abiotic and biotic factors in studies examining the role of landscape composition in services provided by agroecosystem. If one only looks at the drivers of natural enemy abundance, the strongest drivers of biological control potential would appear to be particular habitats within the landscape. However, analysis of our biological control assay experiments reveal that biological control potential was most strongly correlated with biotic (SBA abundance) and abiotic (drought stress) factors.

#### *Biotic prey availability*

Our results did support our expectation that biological control would be higher where pest densities were higher. We hypothesize that this is due to aphidophagous predators navigating with and toward plant volatiles emitted in response to SBA feeding (e.g. Sasso et al. 2009). Predators may also be responding to honeydew odors or SBA alarm pheromones (Hatano et al. 2008, Verheggen et al. 2009). While increasing pest densities may seem counterintuitive to supporting control of those pests, these findings support the notion that successful and

sustainable conservation biological control effects with indigenous and naturalized natural enemies requires stable prey resources.

#### *Abiotic conditions*

Contrary to our initial expectations, we found reduced moisture availability, as measured by increasing drought stress scores, to be associated with increased biological control potential. Moisture availability could be altering plant-insect interactions through a variety of pathways, including changes in the host plant and/or SBA herbivory – which would have implications for predators at higher trophic levels through bottom-up amplification. Previous research indicates that increasing drought stress can lead to increased crop pest feeding and abundance (Koltunov and Andreeva 1999). Thus reduced moisture availability could aid natural enemy orientation by supporting higher SBA densities.

We also found evidence for the importance of temperature, as measured by cumulative growing degree days, in biological control potential of SBA through two significant crossover interactions. Our finding that aphid suppression is higher in fields where growing degree days are lower and grassland in the landscape around soybean fields is higher is in line with our hypotheses and previous studies. We expected and found natural enemy abundance to be higher in fields with more grassland in the surrounding landscape (Figure 2A; Gardiner et al. 2009b; Woltz et al. 2012) and higher growing degree day accumulation supports higher rates of SBA growth (McCornack et al. 2004).

Yet we also found that biological control potential is higher when growing degree days are lower and predator abundance is lower. While this may seem initially counterintuitive, this finding can be seen as an extension of the same explanation. Our finding that biological control potential could be higher when predator abundance is low could be explained by intraguild predation.

Common known generalist predators in the soybean agroecosystem in the upper Midwest US are known omnivores. Previous research using SBA and their predators in soybean cage experiments found SBA suppression higher in cages with fewer predators, likely due to increased feeding on aphid prey instead of other predators (Gardiner and Landis 2007). Conversely, our finding that biological control potential is lower when predators are low and growing degree day accumulation is high also fits this explanation. SBA may also escape predator control through increased population growth at higher growing degree day levels (McCornack et al. 2004).

#### *Study Limitations*

Overall, the drivers of ambient SBA generalist predator abundance in the WI soy agroecosystem did not appear consistent with the apparent drivers of biological control potential in our study. The seeming disconnect between our analyses of potential drivers of soybean predator abundance and biological control potential could be explained by the way measurements were taken. Biological control potential scores were calculated based on assays run over 7-day trials and averaged over multiple weeks within a growing season. Conversely, natural enemy abundance are instantaneous measures of community assemblage on a given day within the season. Therefore methodology could explain why the two analyses arrive at very different conclusions. It may also be due to sampling biases, as sweep net sampling is likely to catch highly motile life stages of natural enemies. This includes adult predators, such as syrphid and chrysopid adults, which do not eat SBA, yet are counted in our study as an indicator of egg laying ability and subsequent larval feeding. Nocturnal predators could also be contributing to SBA biological control, and our diurnal sweep sampling would not reflect their presence.

## Conclusions

Our study results indicate the importance of both crop (corn, small grains) and noncrop (forest, grassland) alternate habitats for supporting generalist predators of SBA in the soy agroecosystem in Wisconsin. Yet our study also indicates the importance of explicitly examining the role of abiotic drivers, specifically temperature and moisture metrics, in biological control services provided by ambient predators. Additionally, the strong positive correlation between SBA abundance and biological control scores indicates the importance of prey availability for sustaining conservation biological control. If alternate habitats are critical for motile natural enemies like SBA predators because of the assumption that they provide prey resources across the landscape throughout the growing season, then explicitly including prey densities as variables, as in our study, can help tease out the mechanisms by which alternate habitats are supporting natural enemies.

Understanding how natural enemies contribute to SBA control is critical for economic reasons, in addition to ecological ones. The estimated value of natural enemy derived pest control in Midwest US soybean fields is \$33 per hectare (Landis et al. 2008). Moreover, the results of our study extend beyond the soybean agroecosystem. Predator taxa that are solely or mostly aphidophagous (Coccinellidae, Syrphidae, Chrysopidae) are commonly found in agroecosystems globally. With the demand for global crop yields increasing, promoting conservation biological control of crop pests could be a way to support demands for increasing yields while supporting biodiversity and beneficial insects in agroecosystems.

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## Tables.

<b>Generalist Predator Abundance</b>		<b>Biological Control Efficacy</b>	
<i>pseudo-R</i> <sup>2</sup> = 0.56		<i>pseudo-R</i> <sup>2</sup> = 0.57	
Fixed Effects	<i>Coefficient (SE)</i>	<i>Fixed Effects</i>	<i>Coefficient (SE)</i>
<b>Other agriculture</b>	<b>1.230 (0.504) *</b>	Other agriculture	-0.355 (0.274)
<b>Corn</b>	<b>1.962 (0.612) **</b>	Corn	-0.172 (0.375)
Soy	0.747 (0.593)	Soy	0.311 (0.332)
<b>Forest</b>	<b>1.715 (0.690) *</b>	Forest	0.335 (0.400)
<b>Grassland</b>	<b>1.322 (0.615) *</b>	Grassland	-0.741 (0.484)
Growing Degree Days	0.453 (0.560)	Growing Degree Days	0.426 (0.267)
Drought Score	0.152 (0.479)	<b>Drought Score</b>	<b>-0.727 (0.281) *</b>
Aphid Abundance	0.534 (0.618)	<b>Aphid Abundance</b>	<b>-1.294 (0.298) **</b>
		Predator Abundance	-0.273 (0.234)
		<b>Growing Degree Days x Grassland</b>	<b>1.240 (0.326) **</b>
		<b>Growing Degree Days x Predator Abundance</b>	<b>-0.485 (0.214) *</b>

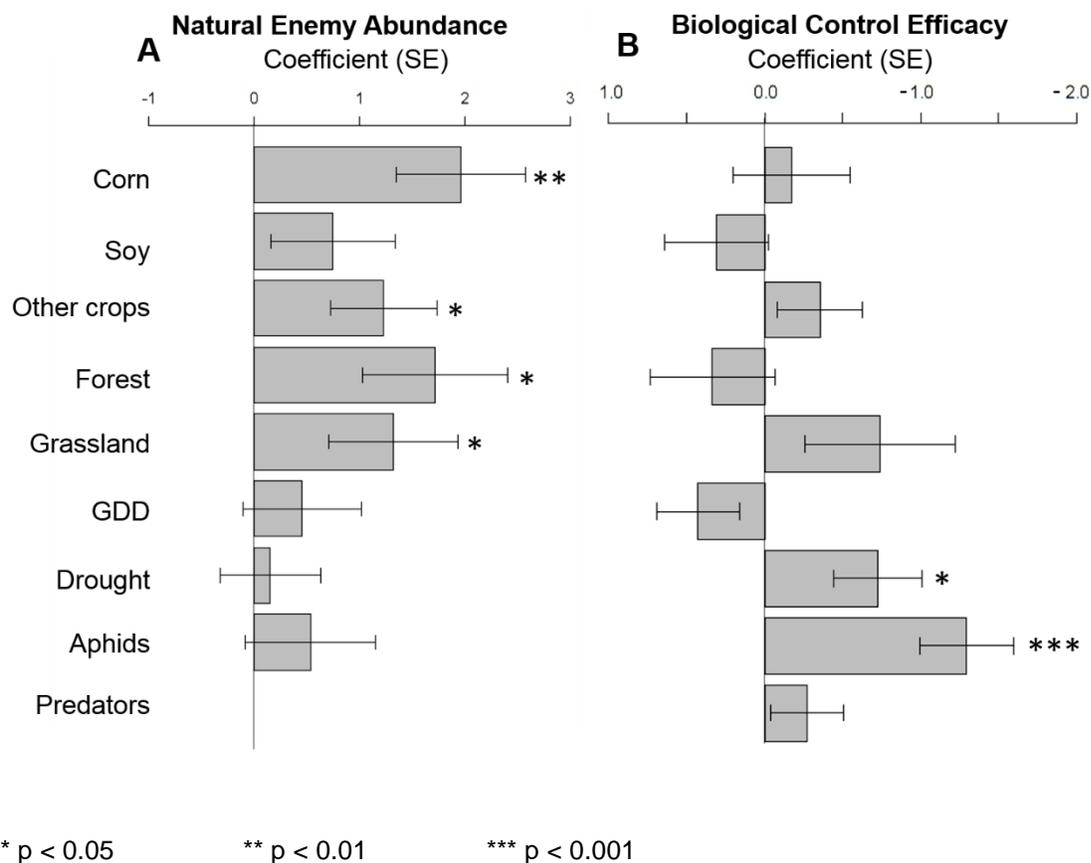
\* p &lt; 0.05

\*\* p &lt; 0.01

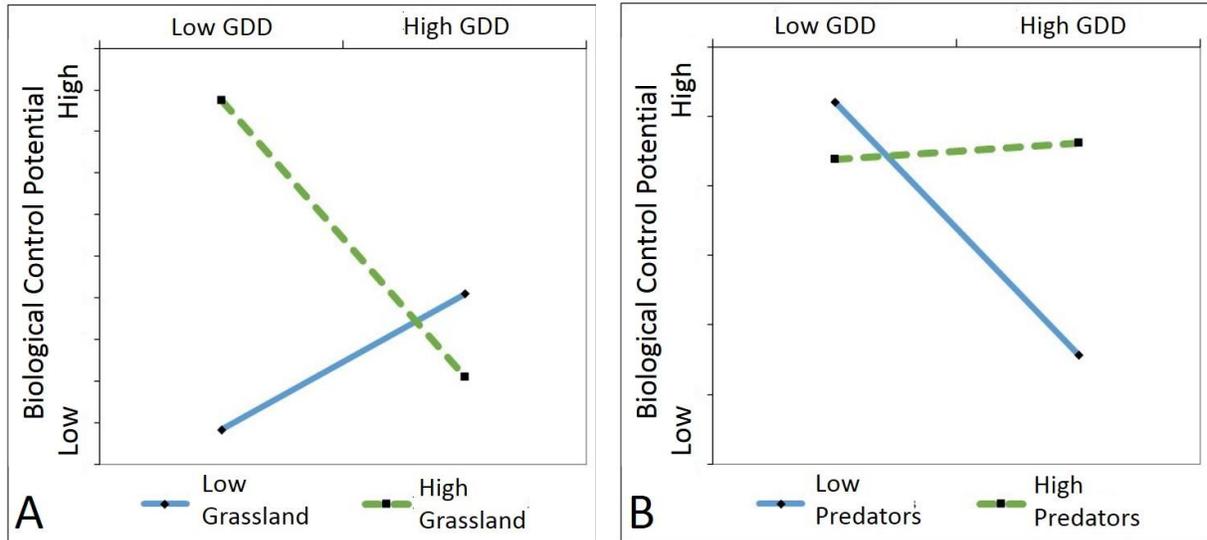
\*\*\* p &lt; 0.001

**Table 1.** Coefficients and standard errors of the fixed effects in our linear mixed effect models for generalist predator abundance and biological control efficacy. Higher aphid suppression is reflected by more negative biological control scores, so negative coefficient scores indicate positive correlations with biological control efficacy.

## Figures

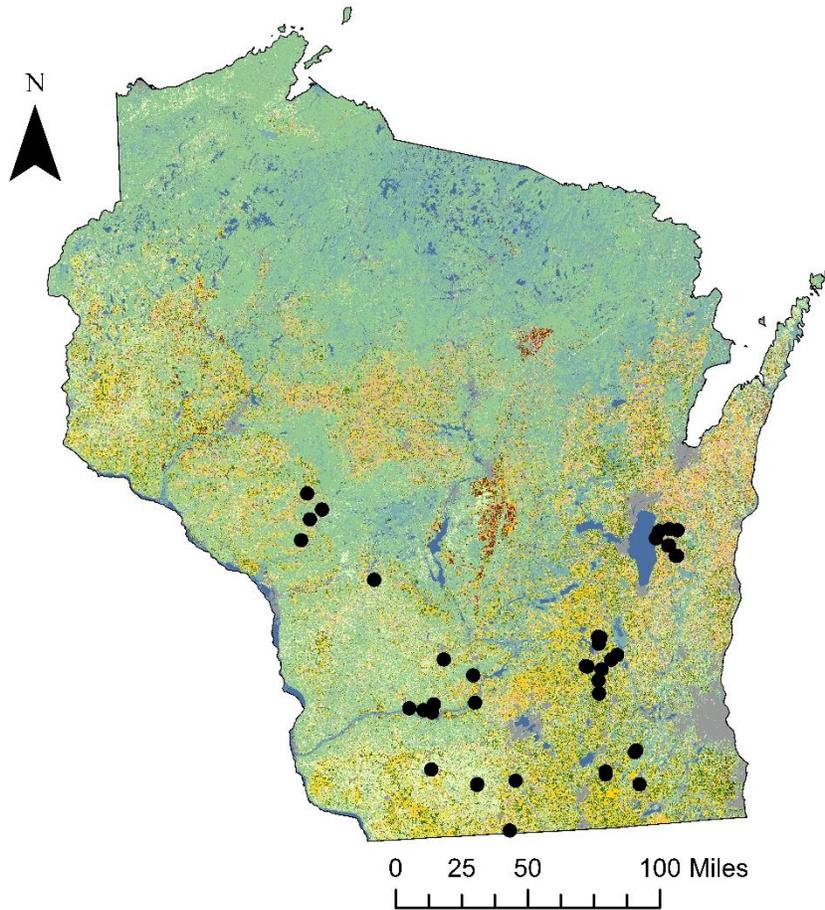


**Figure 1A and 1B.** **Figure 1A.** Coefficients and standard errors of the fixed effects in our linear mixed effect model for generalist predator abundance. Statistically significant associations are marked with asterisks. **Figure 1B.** Coefficients and standard errors of the fixed effects in our linear mixed effect model for biological control efficacy scores. The more negative the coefficient associated with biological control scores, the more positively correlated the independent variable is with biological control efficacy. Statistically significant associations are marked with asterisks.



**Figures 2A-2B.** In our biological control model, two 2-way interactions were significant: growing degree days by grassland (Figure 2A) and growing degree days by predator abundance (Figure 2B). Since the main effects tested were not significant, this is evidence of a crossover effect – wherein the effect of growing degree days on biological control efficacy scores depends on the proportion of grassland in the surrounding landscape and predator abundance (Table 1).

## Appendices



**Appendix Figure 1.** Study sampling locations from 2013 and 2014, displayed over the 2013 USDA Cropland Data Layer (USDA CDL).

## Chapter 4

### Soybean yields influenced by landscape context and insecticide use

#### Abstract:

Landscape context is known to influence crop pest and natural enemy abundance and function in agroecosystems by moderating the flow of resources and organisms across habitats and into agricultural fields to provide biological control services. There is some evidence that this can translate to landscape effects on crop yields through cascading effects on agricultural insect communities. However, previous studies have extrapolated the impact on field-scale yields from findings in small plots or cage experiments. Additionally, there are many non-landscape factors, such as abiotic conditions, that are known to influence insect pests and natural enemies in agroecosystems which could be influencing end of season yields. Understanding how landscape context impacts yield is critical for growers and policymakers, as it is the scale at which growers manage their land and make pest insect management decisions. Thus, our objective was to assess the contribution of landscape composition, field management, and precipitation to field-scale soybean yields in Wisconsin through impacts on soybean insect pests and natural enemies. We used a two-trial approach of intensive and extensive sites, and analyzed our data using linear mixed-effects models.

We found none of our tested variables to have significant relationships with plot-scale soybean yields at the intensive sites. Yet using field-scale yield metrics at the same sites, we found grassland to be positively correlated with increased field-scale soybean yields. At our extensive sites, we found increasing proportions of corn in the landscape surrounding the sampling sites to

be positively correlated with higher soybean yields, as well as grassland and increasing proportions of farmland applied with insecticide in the surrounding county.

No previous studies have traced landscape effects through to crop yield at the field scale. Our results in part demonstrate the importance of using field-scale yields to understand patterns at the scale most relevant to growers. More importantly, our findings show the importance of including a variety of possible factors, not just landscape context, at field- and landscape- scales in analyses of potential drivers of crop yield.

**Introduction:**

Landscape context is known to influence crop pest and natural enemy abundance and function in agroecosystems (Roschewitz et al. 2005, Schmidt et al. 2005). This has been hypothesized to be due to landscapes moderating the flow of resources and organisms across habitats and into agricultural fields to provide biological control services. In support of this idea, previous research has indeed found increased biological control and natural enemy diversity to be positively correlated with semi-natural and natural habitat patches in the landscape surrounding cropland. For example, in a landscape-scale study from 42 canola fields in France, Rusch et al. (2013) found pest abundance and crop damage was influenced in part by landscape complexity. However, the study did not quantify crop damage in terms of end of season yields. Several studies trying to trace landscape effects through to yield impacts have actually studied effects on midseason crop damage, not end of season yields.

Other studies have examined landscape impacts on end of season crop yields but using very small spatial scales or sample sizes, not field-scale yields across a range of commercial farm fields. For example, Ostman et al. (2003) found that barley yields were 23% in fields with ground-dwelling natural enemies of cereal aphids present. However, this study was done using only 10 fields in one region of Sweden during one growing season. Many other studies have extrapolated field-scale yields from findings in small plots or cage experiments. For example, Liere et al. (2015) found evidence that landscape effects can be traced through natural enemy abundance and biological control to changes in yield. However, this experiment was done in experimental cages, not at the field scale. The implications for field-scale yields are uncertain, as it is unclear how well small plot or cage studies extrapolate out to much large spatial scales.

Landscape characteristics are not the only factors impacting crop yields though. There are many non-landscape factors, such as abiotic conditions, that are known to influence insect pests and natural enemies in agroecosystems. Researchers have been studying the connection between climate variability and agricultural production for a long time, and there is evidence that long-term corn and soy yields in the United States can be partially attributed to variation in temperature and moisture conditions in the summer (Lobell and Asner 2003). This is especially true in regions that rely on rain-fed crops, rather than irrigated (Hu and Buyanovsky 2003).

Within-field management is also critical to understanding yield patterns. Farming practices vary widely between farms and across regions, including seed variety and planting dates, fertilizer and nutrient management, pesticide applications, and whether fields are irrigated. These differences lead to variability in crop plant resistance to herbivores or ability to compensate after herbivory damage (Rusch et al. 2013). Across large geographic areas, the combination of landscape composition gradients and environmental gradients, such as growing season weather conditions and farm management, be difficult to disentangle.

The complexity of sorting out the relative contributions of landscape and environmental gradients could explain why the question of whether landscape effects can be traced through influences on natural enemies and crop pests onto crop yield at field scales changes while tested against other potential competing or co-varying drivers had not yet been rigorously tested. Thus, our objective was to assess the contribution of landscape composition, field management, and precipitation to field-scale soybean yields in Wisconsin. Understanding how landscape context

impacts yield is critical for growers and policymakers, as it is the scale at which growers manage their land and make pest insect management decisions.

The soybean agroecosystem is a great study system for this question. Soy is a major commodity crop in the Midwest, the US, and increasing in acreage globally. The soybean aphid (*Aphis glycines* Matsumura [Hemiptera: Aphididae]) is a key pest of soybean (*Glycine max*), which causes yield losses from direct feeding (Ragsdale et al. 2007). Previous research indicates that soybean aphid abundance is influenced by landscape composition. Specifically, soybean aphids have been found to be positively associated with increasing non-crop habitats of agricultural landscapes (Bahlai et al. 2008, Gardiner et al. 2009, Gardiner et al. 2009b, Gardiner et al. 2010, Woltz et al. 2012). Additionally, insect predators of soybean aphids in soybean have also been found to be influenced by landscape context. Increased abundance and diversity of generalist insect predators of the soybean aphid have been found to be correlated with increasing proportions of grasslands and other non-forested semi-natural habitat in the surrounding landscape (Gardiner et al. 2009b; Woltz et al. 2012).

We specifically hypothesized (1) Soybean yields would be higher in fields with higher proportions of agriculture and grasslands in the surrounding landscape, due to previously studied associations between soybean insect predators and these land cover categories (Gardiner et al. 2009b; Woltz et al. 2012). We also expected (2) Soybean yields would be lower in fields with higher proportions of soy and forest in the surrounding landscape, because these habitats containing the obligate hosts of soybean aphid, including buckthorn (*Rhamnus* spp.), an understory tree common in Wisconsin forests that is the overwintering and primary host of soybean aphid (Rogers et al. 2008). (3) Soybean yields would be higher in fields with higher

growing season precipitation, as previous research found yields to be higher under wetter conditions (Lobell and Asner 2003).

## **Materials and Methods**

### ***Extensive sites***

We collected grower-reported field-scale yields and field management information about 74 commercial soybean fields, representing a wide range of landscape context and climatic conditions across 23 counties in Wisconsin, between 2011 and 2014 (Appendix Figure 1). Geographic positioning (GPS) coordinates were recorded at each sampling location.

### *Crop yields*

End of season field-scale yields (bushels/acre) were provided by growers after their seasonal harvest.

### *Field Insecticide Use*

For extensive sites, we surveyed participating growers about their field management practices. They provided information about the soybean field's planting date, seed variety used, whether and when seed treatments were used and which kinds/concentrations, if fertilizer was applied and when, whether and when herbicides were used and which kinds/concentrations, and whether and when insecticides were used and which kinds/concentrations. Since our study focused on tracing landscape effects through soybean insect pests and natural enemies, we chose to focus on insecticide use in the field. Each field's insecticide application information was used to calculate field insecticide use, using a modified Environmental Impact Quotient (EIQ) score (Eshenaur et al. 2015). An EIQ approach allows comparisons of whole-season pesticide applications between fields, as the formula calculates a score from the environmental and health impacts of pesticides based on the specific active ingredients, rather than simply comparing volumes of chemicals

applied (Kovach et al. 1992). We calculated field insecticide use for each extensive site by taking the EIQ score of each field based on all of the insecticides used and reported in that field during the growing season.

#### *County insecticide use*

We also examined the management intensity of the surrounding landscape. We estimated this by calculating the proportion of cropland treated with insecticides in the county surrounding the extensive site, as measured by the 2012 Agricultural Census (USDA NASS 2012). This was the most spatially and temporally refined information available publicly.

#### *Precipitation*

We consider the effect of climatic variability on end of season yields using cumulative July precipitation. Soybean agriculture in Wisconsin is highly impacted by growing season weather conditions, as the majority is rainfed and thus relies on cooperative weather conditions (Hu and Buyanovsky 2003). July is when growers are relying on precipitation to support soybean seed pod development and seed fill. Moreover, summertime precipitation has been theorized to be the dominant factor contributing to inter-annual variation in yields in the Midwest (Chagnon and Hollinger 2003).

We calculated cumulative July precipitation at each extensive field site using Global Historical Climate Network (GHCN) daily precipitation data, accessed through the National Center for Environmental Information and cleaned up for analysis as described in Garcia and Townsend (*in review*). Cumulative July precipitation (centimeters) at each site was calculated using interpolated grids (480 square-meter cells) constructed from surface observation stations. Data and further documentation available at [https://github.com/megarcia/GT16\\_JGRA](https://github.com/megarcia/GT16_JGRA).

#### *Landscape composition*

We determined landscape composition at each sampling site using GPS coordinates and satellite-derived land cover imagery from the Cropland Data Layer (USDA NASS 2014). We imported annual land cover maps into Arc GIS version 10 software (ESRI 2011). We analyzed and aggregated raw land cover class output according to the methods outlined in Chapter 3. Briefly, we calculated the proportion of soybean, corn, other agriculture, forest, and grasslands in a 1.5 kilometer radius circle area around each sampling site. We selected these classes and our spatial scale of interest based on previous research indicating relevance to soybean pests and their natural enemies (Woltz et al. 2012, Gardiner et al. 2009a). “Other agriculture” included non-corn and non-soybean annual crops and perennial non-grassland crops, such as small grains, alfalfa, and beans. “Forest” included deciduous, evergreen, and mixed forests. “Grassland” included both managed (e.g., pasture) and natural (e.g., restored prairie) grasslands.

### **Intensive sites**

In 2014, we selected 29 working soybean fields to sample (Appendix Figure 1). We visited each of these sites weekly between late June and early September. Geographic positioning (GPS) coordinates were recorded at each sampling location.

#### *Soybean aphid counts*

At each intensive site, we entered the field from the roadside edge at a randomly selected location along the edge. We counted all the soybean aphids on 5 plants at four different stations (at the corners of a 20 x 20 m square), a minimum of 50 m from the edge of the field, for a total of 20 whole-plant counts per field. This sampling method was used to match the standard practice for SBA monitoring by growers, crop scouts, and extension professionals (e.g. Ragsdale et al. 2007). We recorded the soybean growth stage of each plant examined and calculated a field

average (Licht 2014). We then calculated end of season cumulative aphid days (CAD), which represents a season-long metric of average soybean aphid counts per plant, for inclusion in analyses.

#### *Biological control assays*

At each of the intensive sampling sites, biological control clip-cage assays were established on the perimeter of the soybean aphid sampling area. Biological control assays were conducted as described in Chapter 3. Briefly, four pairs of clip-cages with 10 adult soybean aphids were established, and assays were conducted three times per site. Biocontrol control potential was calculated as a biological control index score from assay results by the equation:

$$\text{Biological control index (BCI)} = \frac{\text{SBA}_{\text{open, final}} - \text{SBA}_{\text{closed, final}}}{\text{SBA}_{\text{open, initial}} - \text{SBA}_{\text{closed, initial}}}$$

Thus, the lower the BCI score calculated per clip-cage set, the higher the biological control potential. BCI scores were averaged each week across sets of clip-cages, and BCI scores were averaged at the end of the season, to calculate a seasonal average per field.

#### *Crop Yields*

For each intensive site, end of season field-scale yields (bushels/acre) were provided by growers after the growing season ended. Additionally, we harvested small standardized quadrats (1 meter by 1 meter) from each field, taken near the soybean aphid sampling stations. Within each quadrat, all aboveground biomass was harvested. We measured: 1) biomass wet weight (reproductive and vegetative), 2) biomass dry weight (reproductive and vegetative), 3) total dry seed weight, and 4) the weight of 100 dry seeds.

#### *Precipitation*

We calculated cumulative July precipitation in centimeters at each intensive field site using the GHCN daily precipitation dataset, accessed and calculated as described above for our extensive field sites.

#### *Landscape characteristics*

We calculated land cover metrics using the same methods and categories for the intensive sites as the extensive sites, described above.

#### *Data analyses*

Four yield metrics were used the response variables for intensive sites: (1) grower reported field-scale yield (bushels/acre), and the plot-scale yield metrics from the quadrat harvests: (2) total seed dry weight, (3) total number of seeds, and (4) weight of 100 dry seeds. Our fixed effects in the models were: landscape variables (proportions of soy, corn, other crops, grassland, and forest), cumulative July precipitation, cumulative aphid days (CAD), and biological control index scores (BCI). For extensive sites, the response variable was grower reported field scale yield (bushels/acre).

To analyze yield patterns at our study sites, we fit linear mixed effect models to analyze yield patterns using the *nlme* package in R statistical software (R Development Core Team). All models included landscape variables (proportions of soy, corn, other crops, grassland, and forest) and cumulative July precipitation as fixed effects. Intensive site models also included cumulative aphid days (CAD) and biological control index scores (BCI) as fixed effects. Extensive site models also included field insecticide use, as calculated by our modified environmental impact quotient scores, and county insecticide use. All fixed effects were centered and scaled. As random effects in all models, we included a spatial correlation term from the site's longitude and latitude, which can help identify which variables are driving responses

(Meehan and Gratton 2015). Our extensive site model also included year as a random effect. We calculated model fits using a pseudo  $R^2$ , determined by comparing the squared correlation of our observed data with the fitted model predictions for each data point.

## Results

### *Intensive sites*

We examined the correlation between quadrat harvest plot-scale yields and field-scale yields from our intensive sites using Pearson's product-moment correlations. Total dry seed weight harvested from the plots was the correlated with field-scale yields from the same fields ( $r=0.492$ ,  $n=20$ ,  $p=0.027$ ) (Appendix Figure 2). Field-scale yields were not correlated with the total number of seeds harvest from plots ( $r=0.301$ ,  $n=20$ ,  $p=0.197$ ) or the weight of 100 seeds per plot ( $r=0.070$ ,  $n=20$ ,  $p=0.770$ ) from the same sites. So we focus on dry seed weight as the most appropriate plot-scale yield metric for future discussion.

We found plot-scale soybean yields not to be significantly correlated with any of our tested variables at the intensive sites, as measured by total dry seed weight, using a cutoff of  $p<0.05$  (pseudo- $R^2 = 0.21$ ) (Figure 1A, Table 1). Similar results were found using the other plot-scale yield metrics that we measured from the quadrats at the intensive sites (Table 1). However, using grower reported field scale yields, we found increased field-scale soybean yields to be positively correlated with grassland in the surrounding landscape ( $p=0.0009$ , pseudo- $R^2 = 0.89$ ) (Figure 1B, Table 1).

### *Extensive sites*

We found field-scale soybean yields at the extensive study sites to be significantly correlated with four tested variables, using a cutoff of  $p<0.05$  ( $n=74$ , pseudo- $R^2 = 0.51$ ) (Figure 2, Table 2).

Increasing proportions of corn in the landscape surrounding the sampling sites was positively correlated with higher soybean yields ( $p=0.001$ ), as was grassland ( $p=0.030$ ) (Figure 2, Table 2). Increasing proportions of farmland applied with insecticide in the surrounding county was also positively correlated with higher soybean yields ( $p=0.005$ ) (Figure 2, Table 2).

## **Discussion**

### *Landscape context*

Our results supported our hypothesis that increasing grassland in the landscape is strongly associated with higher field-scale yields. This finding was consistent in both our intensive and extensive site analysis. Additionally, our findings show soybean yield was also positively associated with corn. A possible reason for these associations is that these land uses provide resources for soybean insect natural enemies (Gardiner et al. 2009b; Woltz et al. 2012). Generalist predators, especially ladybird beetles, have been shown to play a key role in suppressing soybean aphid populations in the Midwest US (Costamagna and Landis 2006, Costamagna et al. 2007, Costamagna et al. 2008). Ladybird beetles, in particular *Coleomegilla maculata*, are known omnivores that take advantage of pollen resources in corn fields, tracking resources across agricultural landscapes throughout the growing season (Elliott et al. 2002). Perennial grasslands in the landscape could also be providing a habitat with less frequent and intense disturbances than agricultural land uses in the form of tillage, harvests, and pesticide applications (Landis et al. 2000). Contrary to our second hypothesis that yields would be lower in fields surrounded by higher proportions of soy and forest, our findings at the intensive or extensive sites did not support this. A recent study, also in Wisconsin, did find higher proportions of soybean in the landscape to be positively correlated with soybean yields (Liere et al. 2015). One possible

explanation for the difference in results is that their study used small cage harvests and predator exclusion cages, rather than ambient soybean arthropod communities and field-scale yields.

### *Biotic interactions*

Contrary to our hypothesis that soybean yields would be lower in fields with higher CAD, our findings did not support this notion. This finding is somewhat surprising, given the known potential for soybean aphid feeding to cause damage to soybean and potentially yields (e.g. Ragsdale et al. 2007). However, crop damage in soybean does not necessarily lead directly to corresponding effects in yield, due to plant tolerance and compensation (Kucharik et al. 2016).

We also did not find biological control index scores to be a significant indicator of field-scale yield trends. The diversity and abundance of insect natural enemies is broadly considered to increase as noncrop habitat increases (Bianchi 2006) and landscapes can have strong impacts on biotic interactions between natural enemies and pests (Thies and Tscharrntke 1999). However, there may be threshold effects – either in landscape composition or pest densities – above or below which natural enemies cannot act as effective natural pest suppression of crop pests enough to lead to measurable changes in end of season yields. While the biological control assay experiments demonstrated that ambient levels of predators were successfully eating soybean aphid prey, continuing pest colonization or growth could result in no net change at the field or landscape scale (Thies et al. 2005, Roschewitz et al. 2005). Moreover, soybean natural enemies are known omnivores that exhibit intraguild predation, which means that season-long control of pests by natural enemies may also depend on the abundance and community composition of other natural enemies present throughout the growing season. Another possible explanation is

that BCI scores were calculated as a measurement averaged across multiple weeks within the growing season, which might not be a good correlate to end of season yields.

### *Precipitation*

Our results do not support our initial hypothesis that increasing precipitation would be positively correlated with soybean yields. Yet this does not indicate that precipitation, or other climactic factors, are not important contributors to understanding yield patterns. A recent study found that growing season precipitation was positively correlated with soybean aphid abundance (Stack Whitney et al. 2016), but did not track end of season yields. This could indicate that the relationship between precipitation patterns, soybean aphid abundance, and yield is noisy. We did not have data on soybean aphid abundance at our extensive sites. Additionally, while the extensive site study included observations over four years of climatic conditions across a wide spatial expanse of Wisconsin, including a severe drought in 2012 (USDA Economic Research Service 2012), we cannot predict how the patterns we saw will continue under future or no-analog conditions, as the climate changes in Wisconsin.

Conversely, our intensive site analysis included a limited number of observations. These observations came from one sampling year (2014) that did not experience prolonged extreme weather during the growing season. It's plausible that precipitation remains critical for understanding soybean field yields, yet the small sample size or limited range of precipitation experienced in that one sampling year prevented us from finding a pattern in this analysis.

### *Insecticide use at field- and county- scales*

While we found no evidence that field insecticide use, as measured by mEIQ scores derived from insecticide applications, within fields during the growing season correlated with increased yields

at our extensive sites, higher insecticide use in the landscape, measured at the county scale, was strongly positively correlated with increased soybean yields. However, increased corn and soy acreage in the surrounding landscape of fields was not highly correlated with those fields having higher mEIQ scores or being in counties with higher proportions of insecticide treatment. This is potentially contrary to previous studies, which found that landscapes with higher amounts of commodity crops had higher insecticide use (Meehan et al. 2011, Meehan and Gratton 2015). These results indicate that fields situated in higher insecticide landscapes had higher yields are receiving some benefit. This is not unprecedented, as research from Bt corn agroecosystems found widespread use of insecticidal transgenes provided landscape-scale pest suppression, even in fields without the transgene (Hutchinson et al. 2010). While our analyses don't permit causal inferences, we hypothesize two possible mechanisms in the soybean agroecosystem. The first is that fields surrounded by more insecticide use serve as a relative refuge for motile natural enemies compared to surrounding field in the landscape, providing protection from pesticide exposure and potentially prey resources. The second is that these fields have less herbivory over the season, due to reduced pest spillover and dispersal from the surrounding landscape being treated with higher amount of insecticide.

There is reason to be concerned about how to interpret these findings about the positive correlation between insecticide use in the landscape and crop yields. Pesticides can directly and indirectly alter agroecosystem communities, both pests and natural enemies. This is an especially interesting and important question to understand in soybean agroecosystems. Before soybean aphids emerged as a critical exotic pest, growers in Wisconsin and the north central region of the United States rarely applied insecticides to soybean. Less than 0.1% of acreage was treated with insecticides in 2000 (USDA NASS). The soybean aphid invasion has been linked to

a strong increase in insecticide use (Ragsdale et al. 2004). So while soybean yields may be higher in the fields situated in landscapes using more insecticides, the long term consequences for the arthropods in these fields and landscapes is unclear.

While the combination of intensive and extensive site analyses gave us insight into our study phenomena at multiple scales, we acknowledge the limitations of this approach. While we were able to study field-scale yields by conducting surveys and experiments in commercial soybean fields, the underlying environmental conditions at each site, such as topography, management history, and soil characteristics, cannot be accounted for and may have influenced plant responses to herbivory (Machinski and Whitham 1989, Rusch et al. 2013). Additionally, more unaccounted for variability may come from the range of soybean varieties in the study, as some have different tolerance thresholds for aphid feeding (Ragsdale et al. 2011, Hill et al. 2012).

## **Conclusions**

No known previous studies have quantified landscape effects on crop yield at the field scale. Our results in part demonstrate the importance of both crop and noncrop habitats in landscapes to support improved crop yields. Additionally, we found county insecticide use to improve soybean yields, possibly through landscape-scale pest suppression. Finally, our findings underscore the need to study yield effects at field-scales to understand patterns at the scale most relevant to growers and field management decision-making. Understanding how to optimize field-scale crop yields is critical and will only continue to be more so, as the global demand for food increases with population growth.

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## Tables.

Fixed Effects	Intensive Site Yield			
	100 seed weight (g/100 seeds)	Total seeds (n/m <sup>2</sup> )	Dry seed weight (g/m <sup>2</sup> )	Field yield (bushels/acre)
	<i>Coefficient (SE)</i>	<i>Coefficient (SE)</i>	<i>Coefficient (SE)</i>	<i>Coefficient (SE)</i>
Corn	-1.729 (1.906)	-130.441 (191.859)	6.423 (31.104)	6.730 (4.130)
Soy	-1.645 (1.397)	15.393 (142.752)	11.464 (23.143)	-0.850 (3.073)
Other crops	-1.124 (1.417)	-195.077 (145.420)	-7.545 (23.575)	-1.933 (3.130)
Grassland	-1.788 (1.201)	69.518 (121.627)	21.514 (19.718)	<b>11.811 (2.618) ***</b>
Forest	-0.312 (1.715)	-127.820 (173.204)	6.688 (28.665)	-3.494 (3.728)
Cumulative Aphid Days	-0.204 (0.968)	-2.130 (91.569)	3.318 (14.845)	-4.192 (1.971)
Biological Control Index	0.836 (0.788)	24.865 (79.362)	2.750 (12.866)	-0.398 (1.708)
July Precipitation	0.609 (0.979)	-210.287 (96.683)	-11.928 (15.674)	1.443 (2.081)
	<i>pseudo-R<sup>2</sup>=0.19</i>	<i>pseudo-R<sup>2</sup>=0.48</i>	<i>pseudo-R<sup>2</sup>=0.24</i>	<i>pseudo-R<sup>2</sup>=0.89</i>

\* p < 0.05      \*\* p < 0.01      \*\*\* p < 0.001

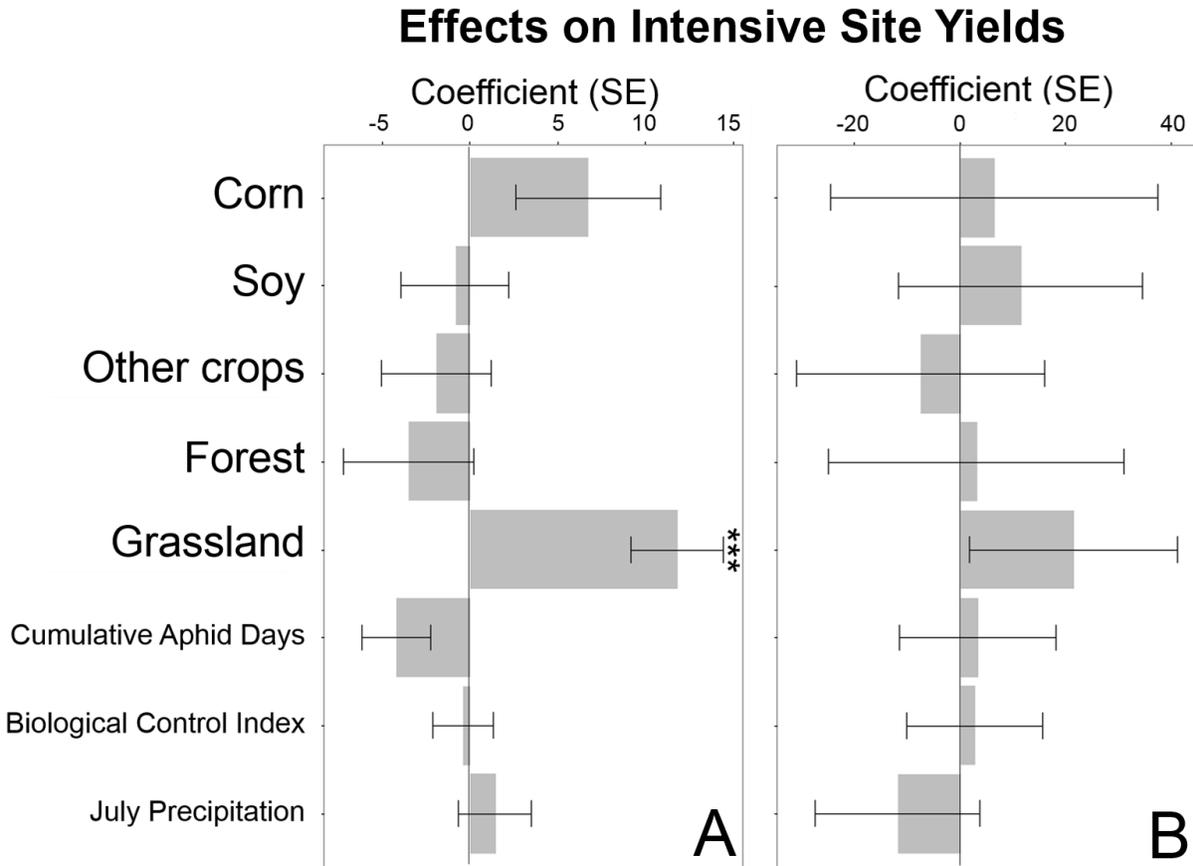
**Table 1.** Coefficients and standard errors of the fixed effects in our linear mixed effect models for intensive site soybean yields.

Fixed Effects	Extensive Site Yield
	Field yield (bushels/acre) <i>Coefficient (SE)</i>
<b>Corn</b>	<b>6.473 (1.929) **</b>
Soy	-0.881 (1.669)
Other crops	1.812 (1.892)
<b>Grassland</b>	<b>5.364 (1.799) *</b>
Forest	2.672 (2.141)
Field Insecticide Use	0.400 (1.288)
<b>County Insecticide Use</b>	<b>5.392 (1.842) **</b>
July Precipitation	0.456 (1.366)
	<i>pseudo-R<sup>2</sup>=0.51</i>

\* p < 0.05      \*\* p < 0.01      \*\*\* p < 0.001

**Table 2.** Coefficients and standard errors of the fixed effects in our linear mixed effect models for soybean yields, as measured by the grower-reported field-scale yield (bushels per acre) at our extensive sites (n=74), using a cutoff of p<0.05 (pseudo-R<sup>2</sup>=0.51). .

Figures.



\* p<0.05 \*\* p<0.01 \*\*\*p<0.001

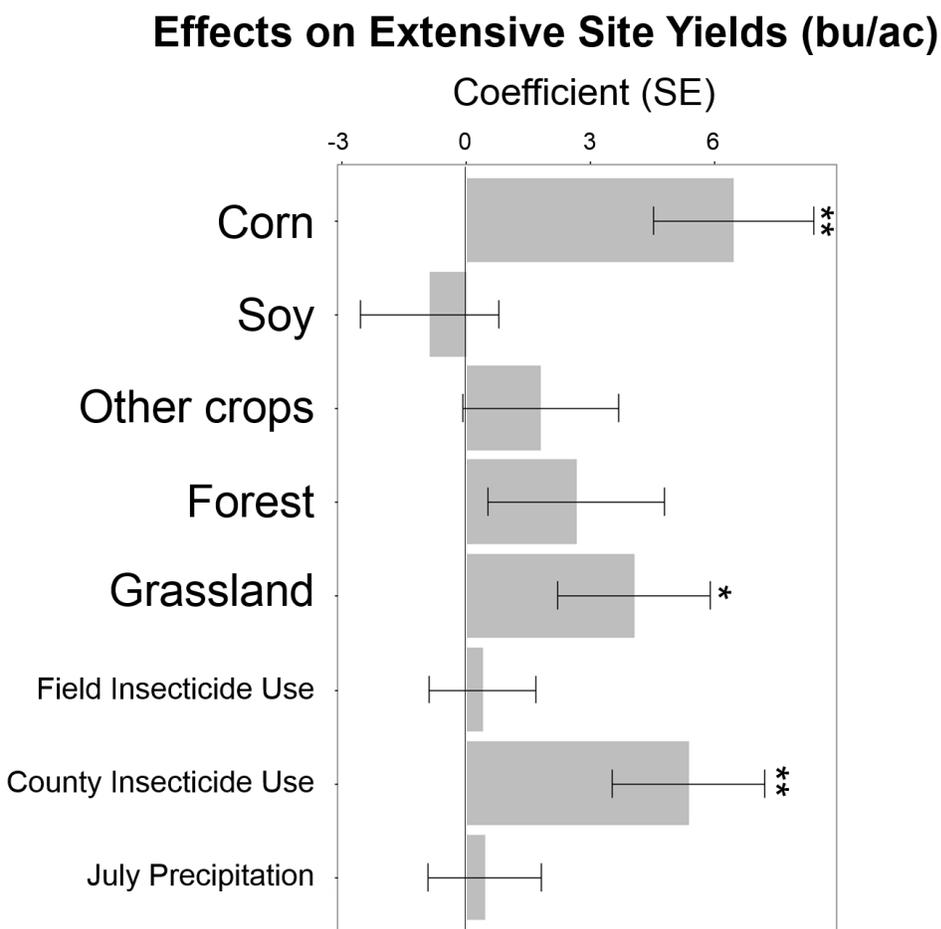
**Figure 1A-1B. Effects on plot- and field- scale soybean yields at intensive sites**

**Figure 1A. Effects on plot-scale (total dry seed weight) soybean yield at intensive sites**

We found no significant correlations between our tested factors and soybean yields, as measured by the total dry weight of seeds harvested from standardized quadrats at our intensive sites (n=20), using a cutoff of p<0.05 (pseudo-R<sup>2</sup>=0.24).

**Figure 1B. Effects on field-scale (bushels per acre) soybean yield at intensive sites**

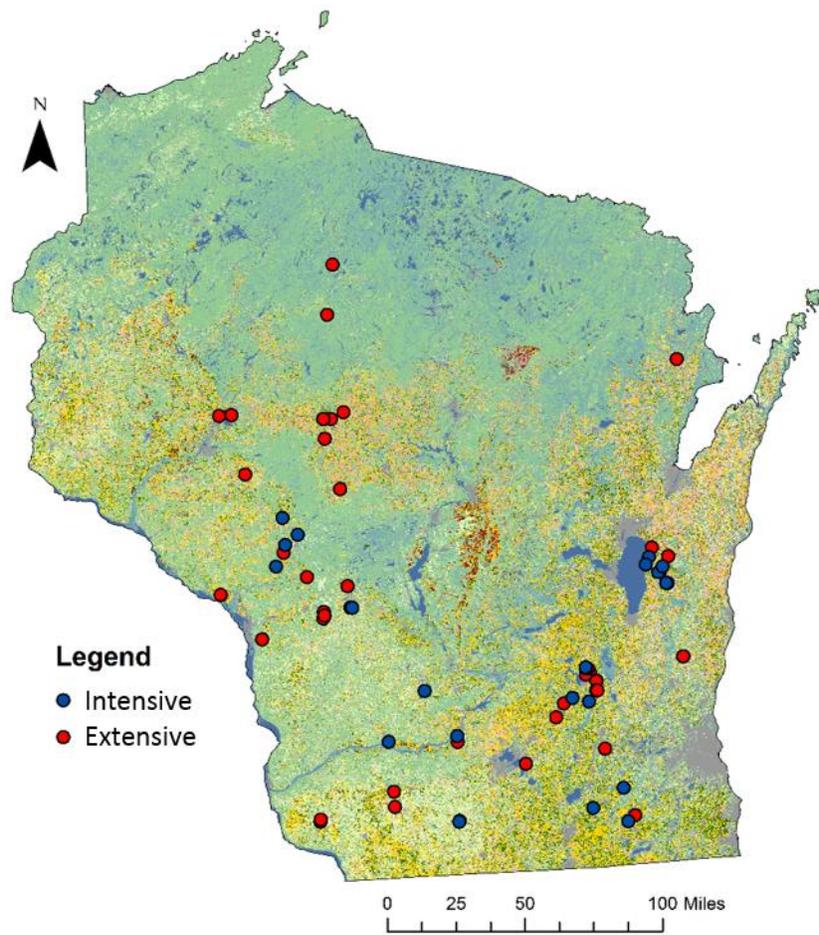
We found increasing grassland in the landscape surrounding our intensive sites to be correlated with soybean yields, as measured by the grower-reported field-scale yield (bushels per acre) at our intensive sites (n=20), using a cutoff of  $p < 0.05$  (pseudo- $R^2 = 0.89$ ).



\*  $p < 0.05$  \*\*  $p < 0.01$  \*\*\*  $p < 0.001$

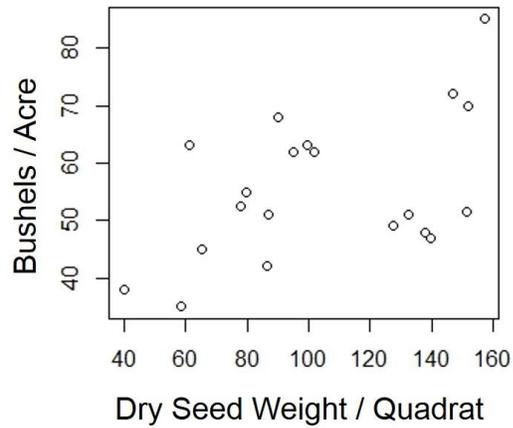
**Figure 2. Effects on field-scale (bushels per acre) soybean yield at extensive sites**

We found increasing corn and grassland in the landscape surrounding our extensive sites to be correlated with soybean yields, as measured by the grower-reported field-scale yield (bushels per acre) at our extensive sites ( $n=74$ ), using a cutoff of  $p < 0.05$  (pseudo- $R^2=0.51$ ). We also found increasing insecticide use in the surrounding county to be positively correlated with soybean yields.

**Appendices.**

**Appendix Figure 1.** Locations of the intensive (n=20) and extensive (n=74) field sites in our study, overlaid on the 2014 USDA Cropland Data Layer.

## Yield at Intensive Sites



**Appendix Figure 2. Correlation between plot- and field-scale yield metrics at intensive sites.**

Total dry seed weight per quadrat harvested was the plot-scale yield metric was correlated to field-scale yield at the same sites at our intensive sites, tested using Pearson's product-moment correlations ( $r=0.492$ ,  $n=20$ ,  $p=0.027$ ).

## **Thesis Conclusions**

As a whole, this work improves our understanding of landscape context as a driver of insect abundance (crop pests and their natural enemies) and insect-derived ecosystem services (biological control and crop yields) in the soybean agroecosystem.

### **Landscape effects can be traced to effects on crop yields at field-scales.**

I was successful in tracing landscape effects to crop yields, as the first study we know of to accomplish this at field-scales. I found that both crop (corn) and semi-natural (grassland) habitats in the landscape support increased yields at field-scales.

### **Landscape-scale insecticide usage could also be traced to effects on crop yields**

I found higher soybean yields to be strongly correlated with insecticide use in the landscape, measured at the county scale. The patchwork of insecticide use in the county could be providing landscape-scale pest suppression, even for growers using fewer pesticides. This finding reveals an effect of landscape unrelated to the traditional view of land cover as proxy for prey resources and supports the continued examination of landscape-scale phenomena in agroecosystems.

### **Abiotic factors are critical to understanding crop pest and natural enemy populations.**

Soybean aphids were more strongly correlated with abiotic factors, specifically seasonal precipitation patterns, than any landscape factors tested. Additionally, natural enemies across taxonomic groupings had significant associations with drought stress, indicating that explicit inclusion of non-landscape factors in insect occurrence and abundance population models is critical. Across large geographic areas and multiple years, disentangling the contributions of

landscape composition gradients and environmental gradients can be difficult. This dissertation is evidence that taking on that challenge resulted in both new findings, of the importance of temperature and moisture metrics tested, and in refined exploration of landscape effects I could have more confidence in.

### **Landscape effects can still be tied to changes in crop pest and natural enemy populations**

Results from each chapter indicate that incorporating landscape context and composition is important to understand patterns of soybean arthropod abundance and function. In fact, we have more confidence in our findings, because in all of our models we included alternate factors, including growing degree day accumulation, drought stress, field management, and pest densities – and incorporated spatial autocorrelation terms. Yet unlike previous studies and theory that would anticipate only semi-natural or natural habitats to be positively associated with natural enemies, I found that both crop and noncrop habitats in the landscape supported increased natural enemy occurrence and abundance in soybean fields. Additionally, soybean aphids appear to benefit from increasing natural habitat (forest) in the landscape.

### **Resource availability is more important than static image of landscape structure**

The heterogeneous responses of specific taxa to landscape features, combined with the strong response of predator abundance and biological control potential assays to prey density, indicates that explicitly tracking resources within the growing season is critical. Moreover, my results support the notion that spatio-temporal variability of resources, like prey, are better predictors of generalist predators and biological control than earlier, more simplistic land cover models.

Resource based models, rather than static annual metrics of land cover, may be a better way of

understanding the contribution of landscapes. Future research should follow dynamic resources across landscapes within growing seasons, to further refine our understanding of how motile predators are tracking prey through time and space.