

Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield

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Abstract. The strength and prevalence of trophic cascades, defined as positive, indirect effects of natural enemies (predatory and parasitic arthropods) on plants, is highly variable in agroecosystems. This variation may in part be due to the spatial or landscape context in which these trophic cascades occur. In 2011 and 2012, we conducted a natural enemy exclusion experiment in soybean fields along a gradient of landscape composition across southern Wisconsin and Michigan, USA. We used structural equation modeling to ask (1) whether natural enemies influence biocontrol of soybean aphids (SBA) and soybean yield and (2) whether landscape effects on natural enemies influence the strength of the trophic cascades. We found that natural enemies (NE) suppressed aphid populations in both years of our study, and, in 2011, the yield of soybean plants exposed to natural enemies was 37% higher than the yield of plants with aphid populations protected from natural enemies. The strength of the trophic cascade was also influenced by landscape context. We found that landscapes with a higher proportion of soybean and higher diversity habitats resulted in more NE, fewer aphids, and, in some cases, a trend toward greater soybean yield. These results indicate that landscape context is important for understanding spatial variability in biocontrol and yield, but other factors, such as environmental variability and compensatory growth, might overwhelm the beneficial effects of biocontrol on crop yield.

Key words: aphids; Aphis glycines; Glycine max; landscape context; pest control; soybean; structural equation modeling (SEM).

INTRODUCTION

Agricultural sustainability depends to a great extent on the ability of predatory and parasitic arthropods (“natural enemies”) to suppress pest populations and rescue crop yield that would otherwise be lost to herbivory. These trophic cascades represent top-down control of insect herbivores by natural enemies resulting in positive, indirect effects on plants (Hairston et al. 1960). In addition to increased plant yield, this form of “biocontrol” can reduce insecticide use (Östman et al. 2003, Zhang and Swinton 2012) and decrease the potential for the evolution of insecticide resistance (Gould 1991). Yet, the strength of trophic cascades in agroecosystems is highly variable (Östman et al. 2001, Thies et al. 2005), and, in some instances, biocontrol and plant yield gains are negligible despite high predator and parasitoid abundances and richness (Finke and Denno 2004). For agriculture to reliably predict the contribu-

tion of trophic cascades to crop protection, it is important to understand factors that affect the local abundance of and interactions between herbivores and their natural enemies.

The strength of trophic cascades can vary depending on the spatial context in which the system occurs (Thies and Tscharntke 1999). Local arthropod population dynamics have been shown to vary with landscape context (Wissinger 1997, Tscharntke et al. 2005a). For example, in agriculture, crop fields set within “complex” landscapes (i.e., landscapes with a large proportion of natural or seminatural habitats) generally support higher local density and diversity of natural enemies than more simplified (less complex) landscapes (Tscharntke et al. 2005b, Bianchi et al. 2006, Chaplin-Kramer et al. 2011). The surrounding habitats may offer food and habitat resources, and overwintering sites (Landis et al. 2000, Tscharntke et al. 2012) that complement those available in the local crop habitat and, through spillover, can increase the local abundance and diversity of natural enemies (Schellhorn et al. 2014). Increased local abundances of natural enemies could result in greater biocontrol and indirectly benefit plants through reduced damage or increased yield. While

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previous studies have addressed the effects of landscape context on the abundance and diversity of natural enemies and insect herbivores (Steffan-Dewenter et al. 2002, Roschewitz et al. 2005, Schmidt et al. 2005, Werling et al. 2011), biocontrol services (Landis et al. 2008, Gardiner et al. 2009), insecticide use (Meehan et al. 2011, Larsen 2013), and crop damage (Thies and Tscharrntke 1999, Den Belder et al. 2002, Thies et al. 2003), few have been able to quantify landscape effects on crop yield. Because crop damage does not necessarily translate to variation in yield due to plant tolerance and compensatory growth (Whitham et al. 1991, Strauss and Agrawal 1999), the indirect effects of landscape composition on crop yield are difficult to predict. Furthermore, because of differences in farm management practices across landscapes (e.g., fertilizer and pesticide uses, watering regime, seed source), which can affect plant resistance and compensation to herbivore damage (Altieri and Nicholls 2003, Rusch et al. 2013), it is usually very difficult to detect any relationship between landscape context and crop yield.

In this study, we aimed to examine the effects of arthropod natural enemies on biocontrol of soybean aphid and soybean yield, and to determine if the strength of these trophic cascades varies with landscape composition. We used a structural equation modeling framework to tease apart the pathways by which landscape composition influences yield gains (Fig. 1A). Specifically, we asked: (1) Does exposure to natural enemies influence insect herbivore population sizes and crop yield (i.e., is there a trophic cascade?) and (2) does landscape composition influence the strength of the trophic cascade through variation in natural enemy abundance? While simply measuring ambient levels of natural enemy abundance, herbivore abundance, and yield in fields of varying landscape context can suggest causal relationships between variables, this method does not allow us to quantify the degree of biocontrol and yield (necessary components for quantifying the strength of trophic cascades). Therefore, in this study, we manipulated natural enemy abundances using exclosures within soybean fields and calculated the effect sizes of pest populations and crop yield (i.e., log-ratio of uncaged vs. caged treatments). This experimental approach allowed us to test the hypothesis that the strength of trophic cascades is dependent on landscape context.

METHODS

Study system

This study was conducted in soybean (*Glycine max*) fields in southern Michigan (MI) and Wisconsin (WI), USA, during July, August, and September 2011 and 2012. Soybean is a summer, annual herb, considered to be mostly self-pollinated (Caviness 1966) and is an economically important crop in the United States with a production value of US\$27 billion/year (Ragsdale et al. 2011). One of the most serious soybean pests in the

United States is the introduced soybean aphid (SBA; *Aphis glycines* Matsumura, Hemiptera: Aphididae). Native to eastern Asia, these sap-sucking insects emerge in the spring from their primary host, buckthorn (*Rhamnus* spp.), and can migrate long distances to colonize their secondary hosts, soybean, in late spring/early summer (May–June). Under ideal conditions (approximately 28–30°C, relative humidity 78–80%), SBA can rapidly increase in population sizes (Ragsdale et al. 2004, Schmidt et al. 2012), but population growth rapidly declines as temperatures reach 35°C (Ragsdale et al. 2011). The economic threshold level (pest population level where a control action should be taken to prevent economic loss) on soybeans has been estimated at 250 aphids per plant and when populations are increasing (Ragsdale et al. 2007). Generalist predators such as ladybeetles (Coleoptera: Coccinellidae) and anthocorid bugs (*Orius insidiosus* (Say), Hemiptera: Anthocoridae) are currently the most effective naturally occurring arthropod biocontrol agents of SBA (Fox et al. 2004, Costamagna et al. 2007). Parasitism rates by native and introduced parasitoid species have steadily increased since SBA introduction in the 2000s, but are still usually <10% and inversely correlated with aphid densities (Noma and Brewer 2008, Ragsdale et al. 2011). The soybean/SBA system is an ideal system for understanding factors that affect trophic cascades because wingless SBA have very low dispersal capabilities, making it easy to follow their population growth, and because SBA have rapid reproduction rates, which facilitates rearing of colonies and observing multiple generations of SBA over time within a single soybean generation.

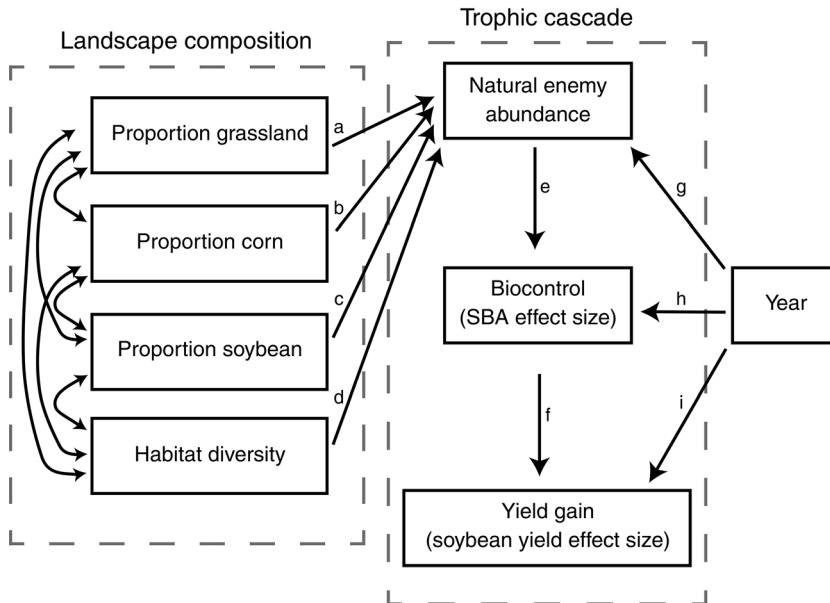
Experimental design

Detailed descriptions of our experimental design can be found in Appendix A. Some differences in sampling effort and experimental design were made across experimental years, but generally followed the protocol described in the following sections.

Site selection.—We used the United States Department of Agriculture (USDA) National Agriculture Statistics Service Cropland Data Layer (USDA 2011) to select commercial soybean fields (hereafter “sites”) that spanned a gradient in the amount of grassland (one of the dominant natural and seminatural habitat in the study area), soybean (the focal habitat), corn (the dominant annual crop type in the study area), and habitat diversity in the vicinity (20 fields in WI and MI in 2011; in 2012, 40 fields in WI and MI; Appendix B). Soybean sites used in this study varied in size from 0.2 to 10 ha, were separated by at least 3 km, and spanned similar gradients in landscape composition in both experimental years.

We used a 1.5-km circular buffer centered in each site to calculate landscape composition metrics. The proportions of corn and soybean in the landscape were calculated as the proportion of the total area within a 1.5 km radius of sites composed of corn and soybeans,

A) Conceptual model



B) SEM results

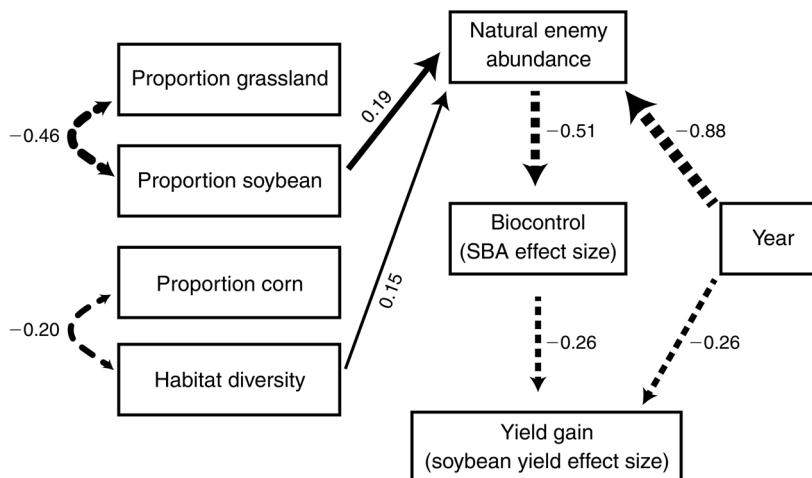


FIG. 1. (A) Conceptual model and (B) structural equation modeling (SEM) results of landscape composition effects on trophic cascades. Single-headed arrows represent causal relationships; double-headed arrows represent correlations. Solid lines represent positive relationships, and dashed lines represent negative relationships. In (A), lowercase letters (a–i) represent relationships between two variables (see *Methods: Data analyses*). In (B), the number along the arrows are boot-strapped, standardized path coefficients, β (arrow widths are scaled to standardized coefficients). Natural enemy abundance represents predator and parasitoid abundances captured in sticky traps in the experimental fields. Soybean aphids (*Aphis glycines* Matsumura; SBA) and yield are represented as effect sizes, log(mean response from “open”/“closed” cages). Closed cages were a treatment where SBA-infested soybean plants were protected from natural enemies, and open cages were where SBA-infested plants were exposed to natural enemies. Model fit: $\chi^2 = 25.7$, $df = 20$, $P = 0.18$, root mean square error of approximation (RMSEA) = 0.06, comparative fit index (CFI) = 0.96.

respectively. The proportion of “grassland” in the landscape was calculated as the proportion of the total area within 1.5 km covered by perennial pasture, hay, and unmanaged/natural grasslands. Habitat diversity was calculated as $1 - \text{Simpson's diversity index } (D)$, using all 41 available vegetated habitat/crop types differentiated in the cropland data layer within the 1.5-km buffers (e.g., alfalfa, switchgrass, apples, deciduous

forest, wetlands, and so on, excluding open water and developed habitats). Habitat diversity was normalized between 0 and 1 for easier interpretation, with 1 being complete evenness and greatest habitat/crop richness.

Natural enemy sampling.—At each site, the abundance of natural enemies (NE; all predatory arthropods and parasitoids) was estimated using yellow sticky cards (Pherocon AM, Trece, Adair, Oklahoma, USA). Dou-

ble-sided sticky cards (15 × 30 cm) were placed at one to three sampling stations within each site and replaced at two-week intervals during the soybean growing season (July to September). In 2011, sticky cards were placed out continuously for three months (six sampling periods; Appendix C), while in 2012, sticky cards were placed out for two sampling periods in late July and early September. Arthropods were identified in the laboratory to the family level and classified as either predators, parasitoids, or herbivores. At each site, the abundances of all parasitoid and predator taxa were summed per card and averaged across sampling stations and sampling periods.

Natural enemy exclusion.—To examine the effects of NE on SBA and soybean yield, we set out experimental cages in August to exclude NE from soybean plants (“closed cages” treatments). These plants were paired with uncovered (2011) or partially covered (2012) plants (“open cages” treatments) with no-see-um netting (Kaplan Simon, Braintree, Massachusetts, USA). Costamagna et al. (2008) directly tested the effect of enclosing soybean plants in Michigan using similar no-see-um netting cages in 2004–2005 and found no significant effect on soybean total biomass or seed yield in either year. In 2011, we planted our experimental plants in small gardens within soybean fields, using a single variety of soybean and fertilizer across sites. In efforts to increase our sample size in 2012, we doubled the number of sites to 40 soybean fields in 2012. However, due to the large amount of manual labor needed to maintain the gardens, in 2012, we used existing soybean fields planted by farmers and, consequently, plant variety and fertilization patterns were not uniform across sites. Prior to setting out cages, all detectable NE were removed manually from experimental plants. The starting densities of SBA on plants varied across years. In 2011, ambient densities of SBA were used as starting densities (initial mean SBA density in closed cages treatment was 49.16 ± 7.22 SBA per plant per site [shown are means \pm SE]; initial mean SBA density in open cages treatment was 69.21 ± 19.13 SBA per plant per site; paired *t* test of initial log-transformed mean SBA densities between treatments $t_{19} = -0.03$, $P = 0.97$). In 2012, to minimize variation in the starting densities of SBA, we removed all aphids from the experimental soybean plants and inoculated each plant with 20 SBA from colonies reared inside large (2 × 2 × 2 m) cages at our field experimental stations in MI and WI. In both years, SBA surveys were conducted twice in September by counting all SBA on each experimental plant. After the last count, we left all aphids on the plants and removed cages at end of the growing season (late September), when soybean seeds dried naturally. We then harvested the pods from the experimental plants, recorded the seed mass per plant and measured humidity content. We then standardized the mass of our samples by correcting for percent humidity using 13% as the standard (13–15% is the recommended humidity

content for harvesting soybeans (Hurburgh 2008), see Appendix A for details).

Data analyses

To determine whether NE exclusion influenced SBA densities and soybean yield (i.e., whether there was a trophic cascade), we performed a series of paired *t* tests. The predictor variable was cage treatment (open vs. closed cages) and the response variables were SBA densities and soybean mass, per plant per sampling station per sampling period and per site. We performed separate *t* tests for each experimental year (four paired *t* tests in total) because we suspected yearly variation of NE abundances to affect SBA densities and soybean yield. SBA densities were log-transformed to meet the assumptions of normality.

To examine how landscape composition influences the strength of the trophic cascade, we performed structural equation modeling (SEM) to determine the direct and indirect effects of landscape composition on “biocontrol” and soybean “yield gain.” We used the log-ratio of SBA densities in open vs. closed cages (i.e., SBA effect size) to quantify biocontrol and the log-ratio of soybean yield in open vs. closed cages (i.e., yield effect size) to quantify yield gain. In our initial model (Fig. 1A), we hypothesized direct relationships between landscape composition (proportion grassland, soybean, and corn, and habitat diversity) and the abundances of NE (Fig. 1A, paths a–d). Because we were interested in quantifying SBA suppression by NE, we hypothesized a relationship between NE abundance and SBA effect size (Fig. 1A, path e). Finally, because pest suppression can influence yield, we hypothesized a relationship between SBA effect size and soybean yield effect size (Fig. 1A, path f). We did not include direct relationships between landscape composition and SBA effect sizes because our experiment was conducted in late in the season (August) where variation in SBA densities are more likely due to factors such as predation pressure rather than colonization from the surrounding landscape. Our unit of replication was the site; therefore, all responses were averaged across sampling stations and sampling periods per site and per year. Because the ratio of sample size to number of parameter estimates was less than the suggested ratio of five (Grace 2006), we combined data from both experimental years and across all sites in WI and MI into one analysis. However, to account for any methodological or environmental differences across years, “year” was included as an exogenous variable in the model influencing NE abundance (path g), SBA effect size (path h), and soybean yield effect size (path i). All analyses were performed in AMOS v22 (IBM 2013).

Parameter estimation and model fitting was performed using maximum likelihood (ML) methods. An assumption of ML estimation is that the data are multivariate normal, so we tested this assumption using Mardia’s multivariate normality test (Mardia 1970).

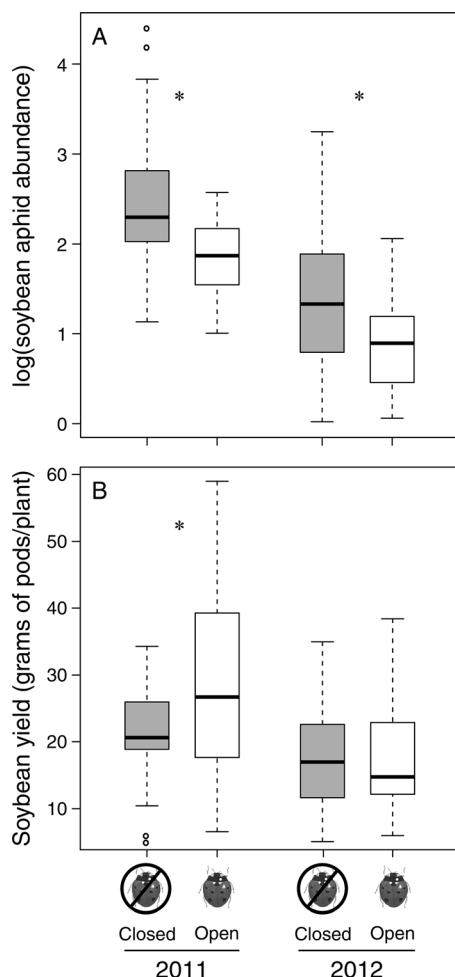


FIG. 2. Boxplots (with medians, lower and upper quartiles [25% and 75%], minimum and maximum values, and outliers displayed) of the effects of natural enemy exposure on (A) soybean aphid (SBA) abundances and (B) soybean yield in 2011 and 2012 (Michigan and Wisconsin [USA] data combined). Gray boxes are closed cages, and white boxes are open cages. Asterisks indicate significant differences ($P < 0.05$) between closed and open cages for a given year.

Results revealed that our data were multivariate non-normal (skewness $b = 12.06$, $P < 0.001$; kurtosis $b = 3.53$, $P < 0.001$); therefore, we used bootstrapping methods for parameter estimation and for generating 95% confidence intervals around parameter estimates ($N = 10000$) because bootstrapping has no distribution assumptions (Byrne 2001, Kline 2011). Another assumption of SEM is linear relationships between variables. We assessed linear relationships between variables by creating bivariate scatterplots of the data. If nonlinear relationships were observed, we included nonlinear terms in the model.

We assessed overall model fit using χ^2 (good model fit when $P > 0.05$), comparative fit index (CFI; good model fit when $CFI > 0.95$), and root mean square error of approximation (RMSEA; good model fit when $RMSEA \leq 0.05$). To improve model fit, we modified our initial

model using a backward and forward stepwise process based on Akaike's Information Criterion (AIC) where nonsignificant relationships were removed (pathways where $P > 0.05$, starting with the greatest P values), or relationships were added based on the residual covariances between variables, and AIC values re-assessed (Grace 2006). Models with lower AIC values are considered better fit models (Burnham and Anderson 2002). For models with similar fits ($\Delta AIC < 2$), we selected the most parsimonious model as our final model (Burnham and Anderson 2002).

RESULTS

Our sites covered a multistate area (Appendix B) and a broad gradient of landscape composition (proportion of grasslands 0.1–0.74, proportion of corn 0–0.57, proportion of soybean 0–0.53, Simpson's diversity 0.46–0.91; Appendix D). Landscape gradients were similar across both experimental years. NE captured on sticky cards included eight predatory families: Coccinellidae (3.87% of total individuals captured in both 2011 and 2012), Syrphidae (6.30%), Dolichopodidae (6.36%), Anthocoridae (35.14%), Nabidae (0.37%), Chrysopidae (0.75%), Hemerobiidae (0.05%), and Lampyridae (2.61%). In 2011, we captured 19 parasitoid hymenoptera families (40.83%), including two families (Aphelinidae and Braconidae) that contain species reported as SBA parasitoids.

Trophic cascades

In 2011, there was a general increase in arthropod abundances across the growing season (Appendix C). The greatest abundances of NE and SBA occurred in September, which coincided with the time that our exclusion experiments took place. NE exclusion treatment had significant effects on SBA abundances and, in 2011, on soybean yield (Fig. 2). During both years, SBA populations exposed to NE (open cages) were significantly lower than SBA populations isolated from their NE (paired t test with log-transformed SBA abundances in 2011, $t_{19} = 3.93$, $P < 0.01$; in 2012, $t_{38} = 4.66$, $P < 0.01$; Appendix C). Furthermore, in 2011, there was a 37% increase in soybean yield when plants were exposed to NE (28.73 ± 3.28 g) compared to plants isolated from NE (20.93 ± 1.76 g; paired t test $t_{19} = -2.81$, $P = 0.01$). However, there was no effect of NE exclusion on soybean yield in 2012 (open cages = 17.17 ± 1.97 g; closed cages = 17.18 ± 1.33 g; paired t test $t_{37} = 0.58$, $P = 0.56$).

Landscape effects on trophic cascades: SEM results

According to the best fit structural equation model ($\chi^2 = 25.7$, $df = 20$, $P = 0.18$, $RMSEA = 0.06$, $CFI = 0.96$; Fig. 1B), there was a positive relationship between landscape composition and NE abundance. Specifically, as habitat diversity (standardized path coefficient, $\beta = 0.15$) and the proportion of soybean ($\beta = 0.20$) in the landscape increased, the abundance of NE in soybean

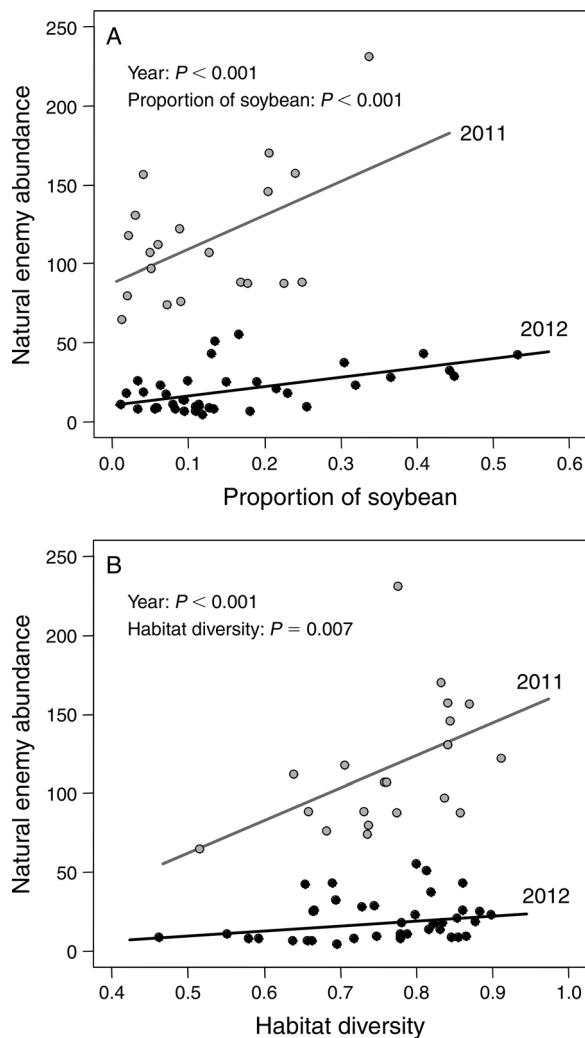


FIG. 3. Natural enemy abundance as functions landscape composition in 2011 (gray) and 2012 (black). (A) The proportion of soybean habitat in the landscape and (B) habitat diversity ($1 - \text{Simpson's diversity } [D]$) were calculated using a 1.5-km buffer centered at each site using the United States Department of Agriculture (USDA) Cropland Data Layer (USDA 2011). At each site, the natural enemy abundances (all parasitoid and predator taxa captured with sticky cards) were summed per sticky card and averaged across sampling stations and sampling periods. Habitat diversity was calculated as $1 - \text{Simpson's diversity index, } D$.

fields increased as well (Fig. 3). There was no relationship between the proportions of corn and grassland in the landscape and NE abundance, although these landscape variables were negatively correlated with proportion of soybean and habitat diversity, respectively (correlation coefficient for soybean and grassland $r = -0.46$; for habitat diversity and corn $r = -0.20$; Fig. 1B).

Lower aphid populations in the open compared to the closed cages (i.e., SBA effect size < 0), would suggest biocontrol by natural enemies. Likewise, higher soybean yield in open compared to closed cages (i.e., yield effect size > 0), suggests a yield gain in the

presence of NE. In our study, NE abundance negatively influenced SBA effect size ($\beta = -0.50$; Fig. 1B). That is, as NE abundance increased, the log-ratio between SBA abundances in open and closed cages increased as well (Fig. 4), indicating that increasing NE abundance was associated with increased aphid suppression. There was also a negative relationship between the effect sizes for SBA and soybean yield ($\beta = -0.24$; Fig. 1B), suggesting that decreasing biocontrol resulted in lower yield gains (Fig. 5).

There was also variability among years in NE abundances (standardized path coefficient, $\beta = -0.88$) and yield effect size ($\beta = -0.29$), where NE abundance and yield effect size, respectively, were greater in 2011 compared to 2012 (Appendix E). Although SBA abundances were also higher in 2011 compared to 2012 (Fig. 2A; Appendix C), there was no year effect on the SBA effect size (Fig. 4). Finally, there were significant indirect relationships between landscape composition to SBA and soybean yield effect sizes (Appendix F). Specifically, there were significant negative, indirect effects of soybean in the landscape ($\beta = -0.10$) and habitat diversity ($\beta = -0.08$) on SBA effect size, but positive indirect effects of soybean in the landscape ($\beta = 0.03$) and habitat diversity ($\beta = 0.02$) on soybean yield effect size.

DISCUSSION

In this study, natural enemies of a crop pest had a top-down, positive indirect effect on crop yield. In addition, the strength of this trophic cascade was greatly

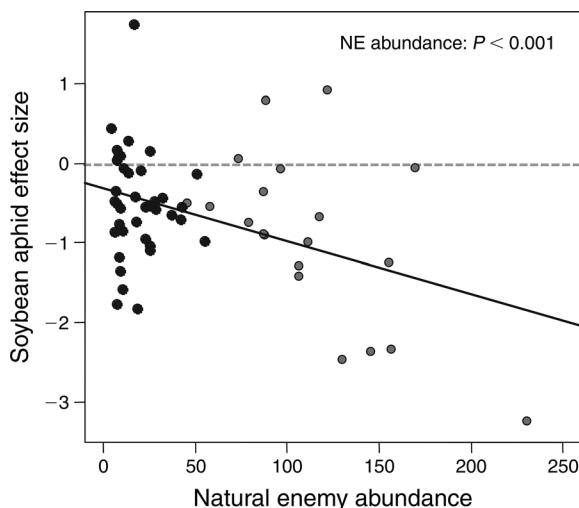


FIG. 4. Relationship between natural enemy (NE) abundance and soybean aphid (SBA) effect size, calculated as $\log(\text{SBA abundance in open/closed cages})$ in 2011 (gray) and 2012 (black). Points represent averaged values across all sampling periods and stations at each site. Gray dashed line represents effect size = 0, where there is no difference in SBA abundances between open and closed cages. Effect sizes < 0 represent lower SBA abundance in open cages. Effect sizes > 0 represent greater SBA abundance in open cages.

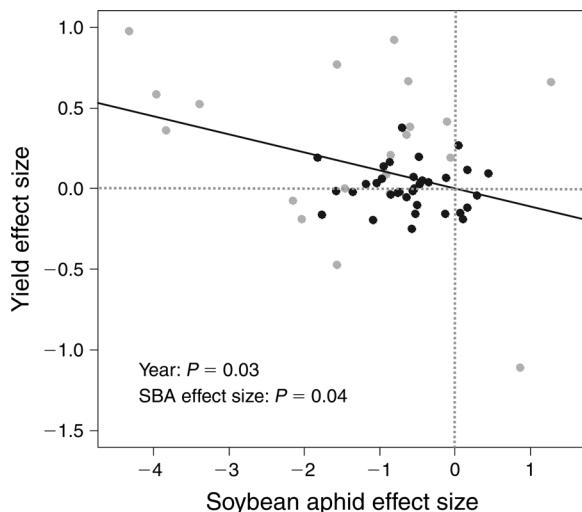


FIG. 5. The relationship between soybean aphid (SBA) and yield effect sizes. SBA effect size calculated as $\log(\text{mean SBA abundance in open/closed cages})$; yield effect size calculated as $\log(\text{mean grams of soybean pods per plant in open/closed cages})$. Points represent effect sizes averaged across all sampling periods and stations at each site. Gray points are effect size values in 2011; black dots are effect size values in 2012. Gray dashed line represents effect size = 0, where there is no difference in the response between open and closed cages. Effect sizes >0 represents greater responses in open cages. Effect sizes <0 represents lower responses in open cages.

influenced by landscape composition thus providing evidence for a positive indirect effect of landscape composition on crop yield. In the past few decades, agricultural landscapes across the central United States have undergone rapid transformations towards row crop production as a result of elevated crop prices (Mehaffey et al. 2012, Wright and Wimberly 2013); these land-use changes are hypothesized to influence biocontrol services with consequences for crop yield. While other studies have reported landscape context to indirectly affect plant damage through cascading effects of natural enemies on biocontrol (Thies and Tscharntke 1999, Thies et al. 2003), and a recent simulation study predicts landscape-dependent cascading effects on crop yield (Bianchi et al. 2013), empirical evidence for the effects of landscape changes on the ability of natural enemies to increase crop yield has remained elusive (Bianchi et al. 2006). To our knowledge, this is the first study to demonstrate, across a broad geographical range, an indirect effect of landscape-context on trophic cascades with measurable yield impacts.

Landscape composition influences natural enemy abundances and biocontrol

In this study, more diverse landscapes in southern Michigan and Wisconsin were associated with a higher abundance of natural enemies, a pattern that matches previous studies (Bianchi et al. 2006, Gardiner et al. 2009). Landscape diversity is often correlated with higher

proportion of non-crop habitats that are expected to act as reservoirs for natural enemies by providing overwintering sites, alternative food sources, and temporally stable refuges (Landis et al. 2000, Bianchi et al. 2006). However, contrary to other studies that show a higher abundance and diversity of natural enemies in landscapes with a greater proportion of natural or seminatural habitat (Tscharntke et al. 2005b, Woltz et al. 2012), we found that the proportion of grassland (the dominant seminatural habitat in southern MI and WI) in the landscape did not influence natural enemy abundances. Instead, like Gardiner et al. (2009), we found that the number and amount of different habitat types (i.e., landscape diversity), rather than the proportion of non-crop habitat, positively influenced NE abundances. Compositional heterogeneity of habitat types might be more important than the amount of natural habitats because different species may require different cover types to complete their life cycles (Fahrig et al. 2011, Meehan et al. 2013). Furthermore, theoretical studies predict that habitat heterogeneity increases regional population persistence by reducing synchrony between patches of the same habitat type (Amarasekare 2008). Accordingly, in our study, NE seemed to benefit more from landscapes with a greater diversity of cover types and not from those with a higher proportion of natural habitats.

Interestingly, there was also a positive effect of the proportion of soybeans in the landscape on natural enemy abundance. These results could, in part, be explained by some natural enemy species that prefer crop habitats over natural (or seminatural) habitats (Tscharntke et al. 2005b). For example, true bugs were one of the most dominant arthropods in our sticky traps (over one-third of all captured NEs) and are considered generalist predators that thrive in agriculture landscapes by feeding on a variety of prey items. In particular, *Orius insidiosus*, which can effectively prevent SBA outbreaks, eats a variety of prey items found in soybean fields (e.g., leafhoppers, thrips, and mites) and can even receive nourishment from soybean pollen (Rutledge et al. 2004). *Harmonia axidiris* is another important predator of SBA that thrives in soybean fields because of its strong aggregation (Donaldson et al. 2007), and numerical response (Rutledge et al. 2004) to SBA densities and its ability to easily disperse between soybean fields (Forbes and Gratton 2011). Thus, by facilitating insect establishment and movement (Margosian et al. 2009), a landscape with a higher proportion of soybean fields may harbor higher SBA populations but could, at the same time, attract and sustain a higher abundance of these generalist, “crop-loving” natural enemies.

We found that both the proportion of soybean in the landscape and habitat diversity positively influenced biocontrol, and therefore, the rescue of soybean yield from herbivory. The relationship between the proportion of soybean in the landscape and habitat diversity at the same scale was hump shaped (Appendix G). This nonlinear relationship suggests that increasing both

variables to maximize biocontrol and increase yield gain is only possible up to a certain point, in this case, when the land cover around a site (1.5 km radius) was ~30% soybean and the habitat diversity index was 0.65. Beyond these values, the benefits of increasing the proportion of soybean in the landscape for biocontrol and yield will be offset by the decrease in habitat diversity in the landscape. Therefore, future modifications to the landscape should consider the effects of multiple landscape variables for biocontrol services and examine the form of the relationships (i.e., linear or nonlinear) among landscape variables.

Trophic trickle: landscape effects on yield gains

Trophic cascades have been reported in other agricultural studies (with alfalfa [Dyer and Stireman 2003, Cardinale et al. 2003] and soybeans [Costamagna and Landis 2006]); however, these studies were conducted in single fields with little opportunity to explore the effects of environmental variation. Our study was performed in multiple fields across two states and across multiple years, allowing us to examine how spatial context can influence the strength of trophic cascades. In our first sampling year, when simply comparing between plants exposed to and isolated from natural enemies across field sites and states, we found a 37% increase in yield when plants were exposed to natural enemies (Fig. 2B). In addition, we were able to detect indirect landscape effects on yield through variation in NE abundances and aphid pressure; however, these indirect effects were small (unstandardized path for proportion soybean $B = 0.07$; unstandardized path for habitat diversity $B = 0.064$; Fig. 1B).

Even though our paired experimental design allowed us to control for inevitable differences within experimental fields and plants, environmental conditions and plant ontogenetic factors may have minimized yield differences between open and closed plants. First, the underlying environmental conditions between each paired cages and across sites (e.g., soil condition, topography, and management history) could have influenced the ability of soybean to offset aphid pressure (Machinski and Whitham 1989, Valantin-Morison et al. 2007, Rusch et al. 2013). If soybeans were planted in sites with fertile soils, increased resource availability could have offset the negative effects of high aphid damage through compensatory growth, minimizing the difference in yield between open and closed cage treatments. Second, differences between treatments may also have been reduced by timing the exclusion experiments late in plant ontogeny. Because biocontrol may be most beneficial to plants during vulnerable times of plant development (Boege and Marquis 2005), our experiments may not have captured the full yield benefits of reduced pest load during early vulnerable plant stages. Lastly, the timing of the experiments may have increased between-field variability in plant responses due to potential differences in early-season SBA infestations. Consequently, because in addition to pest

pressure, yield is often influenced by multiple factors such as nutrient availability, resource competition, plant genotype, and ontogeny (Dale and Polasky 2007, Liss et al. 2013), understanding the full benefit of biocontrol services for yield may require incorporating both local environmental factors as well as landscape variables (and their interactions) into models.

Temporal variation in yield gains

There was temporal variation in soybean yield responses to the cage treatments (Fig. 2); yield gains were greater in 2011 compared to 2012. Across-year differences could be due to several factors; teasing them apart would require further investigation. First, a severe drought affected the Midwest in 2012 (USDA Economic Research Service 2012), which may have impacted the ability of soybean to respond to damage. Additionally, we found lower natural enemy and aphid abundances in 2012 (most likely due to abiotic factors), which could also have influenced yield (e.g., this year, SBA populations were below the economic threshold of 250 aphids/plant; Ragsdale et al. 2007). We also observed a hump-shaped relationship between aphid density and soybean yield (Appendix H), indicating that there is a positive relationship between pest densities and yield at low pest densities (due to overcompensation or attractiveness of larger plants to SBA), but a negative relationship at higher pest densities (Pedigo et al. 1986). If compensatory plant growth occurs at low aphid densities, then this phenomenon could explain why there were small differences in yield between caged and open treatments in 2012 when aphid densities were low. Second, in 2011 we planted a single variety of soybean across all sites, whereas in 2012, we used existing soybean planted by farmers. Because different soybean cultivars have different tolerance levels to SBA infestation (Ragsdale et al. 2011, Hill et al. 2012, Hesler et al. 2013), the use of different soybean varieties across sites may have added variability in responses and masked the effects top-down control on soybean yield in our 2012 experiments.

Conclusions

Our results suggest that the strength of trophic cascades is indeed dependent on landscape context through variation in the abundance of natural enemies. Despite the variation across sites and years, we were able to observe trophic cascades in soybean fields across a broad geographic area in the central United States. We found that landscapes with a higher proportion of soybean and greater diversity of habitats resulted in more NE, fewer aphids, and in some cases greater yield. While these cascades can bring some yield gains to soybean farmers, their effects were relatively small when compared to trophic cascades found in the ecological literature (for example, Costamagna et al. [2008] found between 72% to 90% soybean yield could be rescued by natural enemies at a single site). Moreover, yield is influenced by a variety of other unmeasured factors

(abiotic conditions, local management, soils, or plant genotype), making it difficult to detect the full benefit of biological control amidst this variation. Future studies with larger sample sizes (e.g., Meehan et al. 2011) or experimental designs that can account for additional local variability may be necessary to measure the relatively small effects of landscape composition on yield via arthropod-derived biological control.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–H are available online: <http://dx.doi.org/10.1890/14-0570.1.sm>