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# Contrasting effects of landscape composition on crop yield mediated by specialist herbivores

Ricardo Perez-Alvarez,[1,3] Brian A. Nault,[2] and Katja Poveda[1]

[1]*Department of Entomology, Cornell University, Ithaca, New York 14853 USA*
[2]*Department of Entomology, New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456 USA*

*Abstract.* Landscape composition not only affects a variety of arthropod-mediated ecosystem services, but also disservices, such as herbivory by insect pests that may have negative effects on crop yield. Yet, little is known about how different habitats influence the dynamics of multiple herbivore species, and ultimately their collective impact on crop production. Using cabbage as a model system, we examined how landscape composition influenced the incidence of three specialist cruciferous pests (aphids, flea beetles, and leaf-feeding Lepidoptera), lepidopteran parasitoids, and crop yield across a gradient of landscape composition in New York, USA. We expected that landscapes with a higher proportion of cropland and lower habitat diversity would lead to an increase in pest pressure of the specialist herbivores and a reduction in crop yield. However, results indicated that neither greater cropland area nor lower landscape diversity influenced pest pressure or yield. Rather, pest pressure and yield were best explained by the presence of non-crop habitats (i.e., meadows) in the landscape. Specifically, cabbage was infested with fewer Lepidoptera in landscapes with a higher proportion of meadows likely resulting from increased parasitism. Conversely, cabbage was infested with more flea beetles and aphids as the proportion of meadows in the landscape increased, suggesting that these pests benefit from non-crop habitats. Furthermore, path analysis confirmed that these landscape-mediated effects on pest populations can have either positive or negative cascading effects on crop yield. Our findings illustrate how different pest species within the same cropping system show contrasting responses to landscape composition with respect to both the direction and spatial scale of the relationship. Such tradeoffs resulting from the complex interaction between multiple-pests, natural enemies, and landscape composition must be considered, if we are to manage landscapes for pest suppression benefits.

*Key words:* Brassica oleracea; *crop production; ecosystem services; landscape composition; parasitoid: host ratios; path analysis; pest control; yield.*

## Introduction

Increasing habitat diversity at the local and landscape scales has been acknowledged as an effective strategy to improve pest suppression (Werling and Gratton 2010, Chaplin-Kramer and Kremen 2012, Dassou and Tixier 2016). For example, insect pests can be less abundant in vegetationally diverse landscapes because the concentration and connectivity of crop-food resources are decreased (Rand et al. 2014). Additionally, abundance of arthropod predators and parasitoids has been positively correlated with the availability of non-crop vegetation in the landscape (Chaplin-Kramer et al. 2011b). Such non-crop vegetation can provide complementary resources such as nectar, pollen, alternative food sources, and shelter that allow populations of natural enemies to increase (Bianchi et al. 2006), thus leading to a greater pest suppression (Thies and Tscharntke 1999).

Although positive associations between increasing vegetational diversity and pest suppression have been documented on both local (e.g., on-farm) and landscape (e.g., landscape composition) scales (Gardiner et al. 2009, Chaplin-Kramer and Kremen 2012), most studies have focused on the responses of single pest species. A detailed focus on individual species has proven useful in identifying the underlying ecological mechanisms driving species responses to landscape structure (O'Rourke et al. 2011). However, this approach has limitations because crops are often attacked simultaneously by multiple insect pests that can be differentially affected by local and landscape habitat diversification. For example, insect pest species within the same cropping system may respond to different land cover types and at different spatial scales (Letourneau and Goldstein 2001, Zaller et al. 2008), so landscapes that are managed to reduce one species may increase the abundance of another. Alternatively, an insect pest may benefit from conditions that also favor natural enemies (Thies et al. 2005), thereby offsetting any advantage provided by landscape heterogeneity.

The complexity of interactions among pests and their natural enemies has been shown to influence pest abundance (Martin et al. 2013). Yet, far fewer studies have evaluated the effects of such pest–natural-enemy complexities on crop yield (but see Poveda et al. 2012, Liere et al. 2015). The lack of multiple-pest studies that examine both positive and negative effects of changes in landscape and habitat composition is a major impediment to advancing our understanding of how to design landscapes to optimize overall pest control. Thus, the goal of our work was to address some of these knowledge gaps in landscape effects on pest and natural enemy complexes, by studying the linkages between landscape composition, pest and natural enemy communities, and crop yield.

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[3] E-mail: mrp245@cornell.edu

Landscape-scale pest management requires understanding the effect of landscape composition on natural enemies and pests. Landscapes with large amounts of non-crop habitats (e.g., forest, meadows, and hedgerows) often support higher diversity and abundance of natural enemies than landscapes dominated by crops (reviewed by Bianchi et al. 2006, Chaplin-Kramer et al. 2011*b*). Moreover, it has been postulated that increasing the amount of non-crop habitats in the landscape may have the potential to enhance overall pest control (Rusch et al. 2016), and ultimately crop yield (Liere et al. 2015). As previously noted, evidence for this premise comes mostly from experiments testing the effects of landscape composition on single pest species. However, many pests also benefit from non-crop vegetation at the landscape scale (Tscharntke et al. 2016), so the potential exists for conflicts between landscape strategies that aim to reduce pest populations and those that aim to increase natural enemies. For example, Rusch et al. (2011, 2012) found that landscapes with large amounts of non-crop habitat exhibited higher pollen beetle densities and oilseed rape damage despite increasing parasitism rates. Similarly, multi-pest studies have found contrasting results in how species respond to changes in the proportion of non-crop habitats in the landscape (Zaller et al. 2008), further confounding the patterns emerging between overall pest abundance and landscape composition. Most landscape studies have overlooked these trade-offs, and we are not aware of any empirical studies to date examining trade-offs between multiple insect pests and crop yield in response to changes in landscape composition.

In this two-year study, we examined the effects of landscape composition on the abundance and incidence of a complex of crucifer pests and their parasitoids and determined whether these effects translated into changes in plant damage and cabbage yield (*Brassica oleracea* L. var. capitata). The pest species complex included leaf-feeding caterpillars (*Pieris rapae* L., *Plutella xylostella* L.*, Trichoplusia ni* Hübner), aphids (*Brevicorne brassicae* L.), and flea beetles (*Phyllotreta cruciferae* Goeze, *Phyllotreta striolata* F.). Although these species are all crucifer pests, they differ in their responses to habitat composition, dispersal abilities, and life history (Banks 1998, Hooks and Johnson 2003), providing an excellent opportunity to explore landscape effects in a multi-species system. In addition, cabbage yield is not influenced by pollination, making it a good model system in which to study the effects of landscape composition on crop yield mediated through herbivory. We hypothesized that (1) landscape simplification, through reduced diversity of land cover types and overall increase in the proportion of cropland in the landscape, would positively affect both pest abundance and pest incidence (O'Rourke et al. 2011, Rand et al. 2014). Following other studies investigating landscape effects on natural enemies (Thies and Tscharntke 1999, Chaplin-Kramer et al. 2011*b*), we also hypothesized that (2) parasitoids would respond positively to the proportion of non-crop habitats in the landscape. And last, we hypothesized that (3) a greater proportion of non-crop habitats in the landscape would decrease overall plant damage, and thereby increase crop yield, via indirect effects on both pests (Poveda et al. 2012) and natural enemy abundance (Liere et al. 2015).

## Methods

### *Experimental sites*

The study was conducted in 11 study areas throughout the Finger Lakes Region in New York State, USA, from June to September in 2014 and 2015. Study areas were characterized by either organic or low input annual crops, meadows, patchily distributed forest fragments, and seminatural habitats. Crops in these landscapes mainly consisted of corn, soybean, winter wheat, and crucifers, while seminatural areas included shrubland, deciduous forest, woody wetlands, evergreen forest, and mixed forest. Meadows in this region are composed primarily of native grasses, perennial wildflowers (e.g., *Solidago* spp., *Aster* spp., and *Oxalis stricta*), and introduced cool-season perennial forages such as orchard grass, alfalfa, smooth bromegrass, and white clover (Mohler 1991, Karsten and Carlassare 2002). These perennial forages in the meadows are not maintained for grazing animals, rather they are grown to improve fertility and soil health and may be harvested for animal feed (e.g., alfalfa and clover).

Within each study area, the composition of the surrounding landscape varied at both local and landscape scales. To investigate the effect of local composition on pest and enemy abundance, a pair of experimental fields was established in each study area. This paired design allowed us to select places that varied in local composition (i.e., differences in field margins), while controlling for differences in abiotic conditions and landscape context. Because many crops are rotated annually in this landscape, experimental fields within a study area were not the same in 2014 and 2015. In total, 22 experimental fields sites were sampled in 2014 and 22 other fields were sampled in 2015. The distance between experimental fields within a study area was 0.8 ± 0.3 km (mean ± SD), with a minimum of 300 m, and between study areas was 7.2 ± 2.3 km with a minimum of 2 km.

To quantify the landscape composition surrounding our experimental fields, we measured the proportion of cropland, meadows, and seminatural habitats (for more details, see Appendix S1: Table S1). We chose to measure these landscape metrics because previous studies have shown that they could affect the dynamics and distribution of lepidopteran pests (Poveda et al. 2012), aphids (Woltz et al. 2012) and flea beetles (Banks 1998, Andersen et al. 2005). Across our study areas, cropland cover and the area planted in *Brassica* crops were correlated (Pearson's $r = 0.65$, $P = 0.043$). In addition to calculating land cover proportions, we quantified landscape diversity as Shannon-Wiener index ($H$), using all habitat types surrounding each experimental field (excluding open water and developed habitats). Metrics of landscape configuration (edge density and mean proximity index; see Joshi et al. [2016]) were highly correlated with landscape composition metrics (Pearson's $r \geq 0.65$, $P < 0.02$), and therefore not further considered.

Information on land cover types was derived from the National Agricultural Statistics Service Cropland Data Layer for New York (USDA 2015) and landscape metrics were calculated for each year using the Patch Analysis extension for ArcGIS 10.2 (Rempel et al. 2012). For each experimental field, landscape metrics were calculated at three scales: 250 m (local scale), 500 m (intermediate scale), and

1,000 m radius (landscape scale). These scales were chosen because specialist insects respond strongly to landscape composition at these spatial extents (Chaplin-Kramer et al. 2011*b*). We found moderate correlations among some landscape variables (Appendix S1: Table S2). However, collinearity among landscape predictors was examined, and there were no collinearity problems for any model. All landscape predictors included in the final models had a variance inflation factor (VIF) ≤10 indicating no problematic collinearity among predictors (Montgomery and Peck 1992).

### *Plant material and site design*

Cabbage seeds (*B. oleracea* var. capitata cv. Capture) were sown into organic potting mix (sunshine; Sun Gro Horticulture, Bellevue, Washington, USA) in 128-cell plug trays (54 × 28 cm) and grown in the greenhouse. After seedling emergence, plants were watered every day and fertilized two times per week with an organic fish fertilizer 2-4-1(N-P-K; Neptune's Harvest, Gloucester, Massachusetts, USA) for six weeks and then hardened off outside for seven days prior to transplanting in the field. Plants were eight weeks old when the experiment began.

Within a year, each experimental field consisted of 10 7.5-m rows spaced 0.9 m apart. Plants were spaced 0.4 m apart within rows for a total of 150 plants. Cabbage plants were transplanted across study areas over three consecutive weeks in June 2014 and 2015. Experimental fields within the same study area were planted on the same day. Throughout the growing season, plants were fertilized at transplanting and again one month later using 8-3-3 (N-P-K) granular compost at a rate of 5 kg/100 $m^2$ (Kreher's composted poultry manure; Kreher's, Clarence, New York, USA). Local crop management was homogenous across sites; weeds were removed manually at two-week intervals and no insecticides or fungicides were applied to the plants.

### *Arthropod sampling*

*Insect pests.*—To examine the effects of landscape composition on insect pest populations, we estimated the incidence and abundance of lepidopteran larvae, aphids, and flea beetles in each of the 44 experimental fields. To determine pest incidence, 10 randomly selected plants per experimental field were visually inspected and the percentage of plants infested with the respective pest was calculated at four sampling times per year. We used counts of the proportion of plants infested by more than 10 aphids as a measure of aphid incidence. For lepidopteran and flea beetles, incidence was calculated as the percentage of plants that were infested with at least one lepidopteran larva or one adult flea beetle, respectively. The same plants were used to estimate abundance of lepidopteran larvae and aphids by counting the total number of individuals observed per plant. Samples were collected four times during the season at the seedling, precupping, early head formation, and maturation growth stages (Andaloro et al. 1983). To avoid possible edge effects, plants within 1 m of the edge of the experimental field were not sampled.

Because visual inspection of plants *in situ* is not an accurate method to estimate flea beetle abundance, we used pitfall traps instead. For pitfall traps, we filled a 540-mL clear plastic cup (9 cm diameter openings; Fabri-kal, Kalamazoo, Michigan, USA) with a mixture of water and a few drops of organic, odorless detergent (Unscented Pure Castile Soap; Dr. Bronner's, Vista, California, USA). A total of five traps were placed within the rows between cabbage plants; four traps were located near the corners and one in the center row of the experimental field. Each trap was protected from rain and direct sunlight by an inverted plastic plate (15 cm in diameter) held approximately 10 cm above the trap. Pitfall traps were opened four times throughout the field season at the seedling, pre-cupping, early head formation, and maturation growth stages for 24 h each time. In addition to recording densities of flea beetles using pitfall traps in 2015, we also used yellow sticky cards (15 × 30 cm; BioQuip Products, Grand Rapids, Michigan, USA). One sticky card was positioned at crop height in the center of each experimental field and was replaced biweekly from late June to early September. We found a significant correlation between the number of flea beetles on sticky cards and those in pitfall traps (Pearson's $r = 0.65$, $P < 0.002$), which means that both methods provided similar results for following population trends of flea beetles. Therefore, we used only pitfall trap data from both years in subsequent analyses because they provided the most consistent and complete data set of flea beetle densities over time. Insects collected from visual inspection of plants and pitfall traps were preserved in 70% ethyl alcohol, counted, and identified to the lowest taxonomic level possible, generally genus or species, using a reference collection of insect pests of cruciferous crops maintained in the Cornell University Insect Collection. For better characterization of the overall pest dynamics throughout the growing season, we plotted the mean pest incidence across all experimental fields over time.

*Parasitoids.*—To examine the effects of landscape composition on parasitoids associated with lepidopteran pests, we conducted parasitoid surveys at each experimental field in 2015. Parasitoid abundance was estimated by counting the total number of parasitoid cocoons (i.e., pupa) on 10 randomly selected plants per experimental field. Parasitoid samples were taken concurrently with the visual inspection of plants for insect pests at four sampling times during the growing season. The dominant parasitoid species were identified using diagnostic morphological characters described by Van Driesche (2008). The key parasitoids of *P. rapae,* the dominant lepidopteran pest in our system, are *Cotesia glomerata* and *Cotesia rubecula* (Herlihy et al. 2012), and were the species we focused on in our analyses. While *C. glomerata* is a gregarious parasitoid of several species of pierid butterflies, *C. rubecula* is a solitary host-specific parasitoid of *P. rapae* larvae (Benson et al. 2003). Parasitism of aphids and flea beetles were not included in the analyses because no parasitoids emerged from aphid or flea beetle populations during the sampling period. As with insect pest data, we plotted how parasitoid population densities changed over the sampling period.

### *Plant damage and yield measurements*

To determine the effect of landscape composition on plant damage and crop yield, insect damage and crop biomass was measured in each experimental field in 2014 and 2015. After visual inspection of cabbage for herbivore incidence, the same 10 plants were harvested and assessed for insect damage. Damage was quantified using a modified version of the method of Lim et al. (1986) where a plant is classified into one of the following five categories based on the percent of leaf damage: <5, 5–20, 20–60, 60–80 or ≥80%. Because this method does not account for the damage caused by phloem-feeding insects, a relationship between aphid incidence and plant damage assessed in this manner was not expected. At harvest, crop yield was estimated by weighing the final biomass of a set of 12 mature cabbage heads (>15.2 cm diameter) per experimental field ($n = 12$ in each of 44 fields; Bommarco et al. 2011, Martin et al. 2016).

### *Statistical analysis*

To examine the effects of landscape composition on pest incidence, plant damage, parasitoid : host ratios, and crop yield, we used mixed-effect models in R with the nlme package (Pinheiro et al. 2015). Pest incidence (square-root transformed), parasitoid : host ratios, plant damage (log-transformed), and yield (square-root transformed) were included as response variables. Pest incidence was calculated as the proportion of plants infested by a given herbivore species. Parasitoid : host ratios were calculated by dividing the total number of parasitoid cocoons by the total number of lepidopteran larvae at each experimental field. High parasitoid : prey ratios are indicative of greater biocontrol (Naranjo and Ellsworth 2009, Bowyer et al. 2013), wherein parasitoids strongly affect the target pest density.

Proportion of cropland, proportion of semi-natural habitat, proportion of pastures, and habitat diversity were treated as explanatory variables. For all models, year was also included as a categorical fixed effect to account for any environmental differences across years. In plant damage models, pest incidence was included as an additional explanatory variable. We also used pest incidence and plant damage as fixed effects in the crop yield models. Random effects included experimental fields nested within study areas**.** Our unit of replication was the experimental field ($n = 22$ each year); therefore, all responses were averaged across sampling periods per experimental field and per year.

To construct the models describing the effects of landscape composition on each response variable, we adopted an information-theoretic approach (Burnham and Anderson 2002) in two steps. First, we used the dredge function of the MuMIn package (Barton 2015) to construct models with all combinations of variables and interactions using multiple scales. For each response variable, models were selected by comparing the Akaike information criterion corrected for sample size ($\mathrm{AIC_c}$) values of the full models across scales (i.e., considering the $\mathrm{AIC_c}$ among all data sets). Models with the smallest $\mathrm{AIC_c}$ values were considered to better fit the data (Burnham and Anderson 2002). For models with similar fits ($\Delta\mathrm{AIC_c} < 2$), we selected the most parsimonious set of fixed effects as our final model. We assessed the statistical significance of each explanatory variable and interaction terms (i.e., fixed effects) of the final models by conditional $F$ tests (Pinheiro and Bates 2000). The final models did not include interaction terms since none were found to contribute significantly to the model fit. We also calculated the marginal $R^2$ values for the final models (variance explained by the fixed effects), using the methods detailed in Nakagawa and Schielzeth (2013). Model residuals were graphically inspected to ensure no violation of normality and homoscedasticity assumptions. All final models were tested for spatial autocorrelation in the residuals using the mantel test from the package ade4 (Dray and Dufour 2007). No significant spatial autocorrelation was detected for any model ($-0.06 < r < 0.08$, $P > 0.240$). Subsets of best models for each response variable are presented in Appendix S1: Tables S2, S3, and S4.

In a second step, we estimated the relative importance of landscape variables and year of study in explaining pest incidence, plant damage, and crop yield by summing the Akaike weights of all competing models ($\Delta\mathrm{AIC_c} < 2$) at all scales containing a given variable (Martin et al. 2016). The relative importance is 1 if the variable is included in all competing models and 0 if the variable is not included in any of the competing models. The relative importance represents a measure of evidence across scales that a variable contributes to explaining the response. In the same fashion, we calculated the most predictive spatial scale for each response variable. By summing the Akaike weights across all competing models in which a scale appears, the relative importance of each scale was determined. As previously described, values closer to 1 indicated increased importance of a given spatial scale. The relationships between landscape composition and response variables were plotted at the most predictive scales.

*Confirmatory multilevel path analysis.*—To examine how landscape composition influences crop yield, we conducted a multilevel path analysis (Shipley 2009), evaluating the causal relationships between landscape composition, pest incidence, plant damage, year, and crop yield. Based on the models selected in the analysis described above and our biological knowledge of the system, we hypothesized a direct relationship between landscape composition (proportion of cropland, meadows and semi-natural habitats in the landscape) and the incidence of insect pests (flea beetles, aphids, and Lepidoptera). We also hypothesized that crop yield would be directly related to plant damage. Finally, we hypothesized that insect pests would have a negative effect on crop yield either directly or indirectly, through increased plant damage. We did not include a direct relationship between plant damage and aphids, because the method we used to estimate plant damage does not account for the type of damage caused by phloem-feeding insects. Year was included as an exogenous variable in the model influencing pest incidence, plant damage, and crop yield. Based on the path model constructed following these hypotheses, we identified all possible independence claims (i.e., pairs of variables that are expected to be statistically independent upon conditioning on some other set of variables; see Appendix S1: Table S5). The overall fit of the path models was then tested using Shipley's $d$-separation test for each possible independent claim, and Fisher's $C$ statistics to test whether observed levels of correlation across all independent claims can be explained by random variation. 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 $P > 0.05$), or significant relationships were added, and AIC values reassessed (Grace 2006). Models with lower AIC values are considered to be better fit models (Burnham and Anderson 2002). Path coefficients were calculated as the estimated slopes of a set of mixed effect models (see previous section) fitted by maximum likelihood (ML) methods. To enable the comparison of the relative strengths of the different pathways of the final model, path coefficients were standardized by mean and variance using the function scale in the piecewiseSEM package. We also report standardized path coefficients and statistical significance of other direct and indirect links that were no included in the final path model. These path coefficients were used to calculate and compare the strengths of direct and indirect links among variables. Statistical significance of indirect effects was estimated by using a causal mediation analysis approach (Rijnhart et al. 2017) with the packages lme4 (Bates et al. 2015) and mediation (Tingley et al. 2014). All analyses were conducted using R 3.2.3 (R Core Team 2015).

## Results

### *Insect community*

*Insect pests.*—Across experimental fields, the insect herbivore community was dominated by Lepidoptera (17%), aphids (11%), and flea beetles (55%). Other herbivores such as cabbage maggots (*Delia radicum* L.), thrips (*Thrips tabaci* Lindeman), weevils (*Ceutorhynchus obstrictus* Marsham), leaf-miners (*Scaptomyza flava* Fallén), and crickets (*Scapteriscus* spp.) accounted for <17% of all individuals collected.

A total of 416 caterpillars were collected and identified in the experimental fields, with *P. rapae* as the dominant species (94% of the total caterpillars collected) followed by *P. xyllostela* (5%) and *T. ni* (0.4%). The two most common species of aphids observed on plants were *B. brassicae* and *Myzus persicae* (Sulzer), which made up 91% of all aphids recorded. Finally, 2,098 flea beetles were collected and identified, of which 51% were *P. cruciferae*, 33% *P. striolata*, and 16% of other species of the genus *Chaetocnema.*

We found great variation in pest incidence between years with incidences (mean ± SE) of Lepidopteran larvae 16% ± 5%, aphids 11% ± 4%, and flea beetles 46% ± 7% in 2014. In 2015, the mean incidence of lepidopteran larvae and aphids across experimental fields was 28% ± 4% and 30% ± 1%, respectively, which was threefold higher than in 2014. In contrast, flea beetle incidence in 2015 was on average sixfold lower (average 7% ± 3%) than in 2014 (Fig. 1).

Overall, pest incidence at the seedling, pre-cupping, early head formation, and maturation growth stages also showed great variation among years. In 2014, the average proportion of plants infested by caterpillars was 16% ± 5% at the seedling stage and then decreased to 7% ± 3% at the maturation stage. The incidence of lepidopteran larvae in 2015 had the opposite trend than in 2014, with the highest incidence recorded during the early head-formation stage. As with the lepidopteran data, the average proportion of plants infested by aphids in 2014 was higher (18% ± 6%) at the seedling stage and then decreased (5% ± 1%) by the maturation stage. In 2015, the peak incidence of aphids (60% ± 7%) was recorded during the pre-cupping stage, and then decreased gradually thereafter. The seasonal incidence of flea beetles in both years was similar with higher incidences at the seedling stage (2014, 46% ± 7% and 2015, 17% ± 6%) and then populations declined at the maturation stage (2014, 29% ± 7%; 2015, 2% ± 1%; Fig. 1).

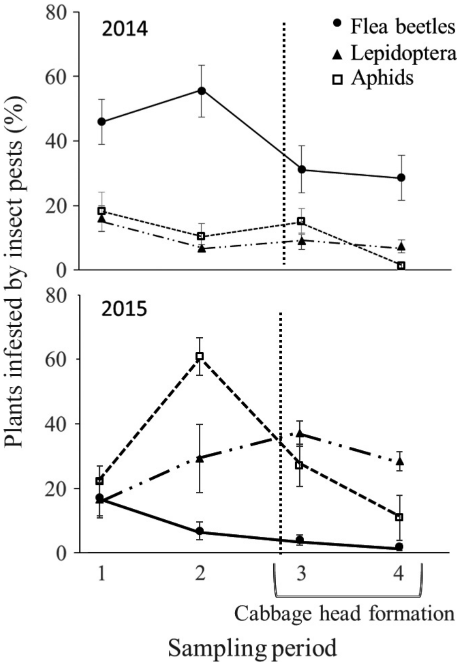

FIG. 1. Incidence (mean ± SE) of flea beetle adults, Lepidoptera larvae, and aphids across all experimental fields in 2014 and 2015. To determine incidence for each insect pest, 10 randomly selected cabbage plants per experimental field were visually inspected at four different times each year and the percentage of plants infested with the respective pest was calculated. Sampling occurred from late June to early September in both years. Cabbage head formation occurred between the third and fourth sampling periods.

*Parasitoids of Lepidoptera.*—In 2015, parasitoid cocoons were collected in 17 of 22 experimental sites. *C. glomerata* and *C. rubecula* were the major parasitoids species attacking *P. rapae* larvae in the study area. Of 331 parasitoid cocoons found in samples, 311 belonged to *C. rubecula* (94%), 19 (6.1%) were *C. glomerata* and 1 case was not identified. Regarding geographic distribution, *C. glomerata* was only present in 2 out of 17 sites. Abundance of *C. glomerata* was low, so it was not included in subsequent analyses. Contrary to *C. glomerata*, the specialist parasitoid *C. rubecula* was detected in 17 of 22 field sites. The parasitoids of the *T. ni* and *P. xylostella* were not investigated because both pests occurred in small numbers in our study.

During the seedling stage, abundance of *C. rubecula* was low but the numbers increased as the season progressed. By the stage of early head formation, there were, on average, 13-fold more parasitoid cocoons per plant than in the seedling stage. At the maturation stage, the number of parasitoid cocoons decreased 35% in the experimental fields relative to the highest peak level recorded in the early head formation stage (Fig. 2). Although there was great within-site variability, parasitoid abundance across experimental fields correlated with the average number of *P. rapae* larvae over the

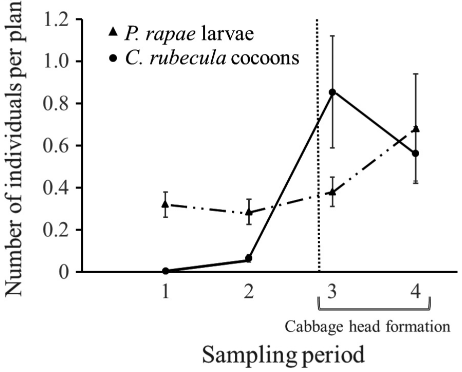

FIG. 2. Abundance (mean ± SE) of *Pieris rapae* larva and its parasitoid *Cotesia rubecula* on cabbage plants across all experimental fields. *P. rapae* larvae and *C. rubecula* were visually sampled on 10 randomly selected cabbage plants per experimental field at four sampling times during the growing season in 2015. Sampling occurred from late June to early September. Cabbage head formation occurred between the third and fourth sampling periods.

first three-quarters of the sampling period (Pearson's $r = 0.68$, $P = 0.001$).

### *Landscape analysis*

The relative importance values of explanatory variables identified year and proportion of meadows, as the most influential variables explaining insect incidence and abundance (Fig. 3). The incidence for all insect pests did not vary with the proportion of cropland or seminatural habitat in the landscape at any scale. Likewise, pest incidence was not affected by habitat diversity regardless of scale. Positive effects of the proportion of meadows at 250 and 500 m radius were found to best explain the incidence of aphids and flea beetles, respectively (Fig. 4a,b). At the 1,000-m scale, we found that the proportion of meadows had relatively low importance in explaining incidence of aphids and flea beetles. In contrast, Lepidoptera incidence decreased in fields surrounded by landscapes with greater proportions of meadows at 1,000 m (Fig. 4c), whereas no effect of the proportion of meadows on Lepidoptera incidence was shown at smaller scales.

We also found a significant effect of the proportion of meadows in the landscape on parasitoid : host ratios and lepidopteran larval abundance. The parasitoid : host ratios were positively influenced by the proportion of meadows at 500 m (Fig. 4d), whereas lepidopteran larval abundance decreased as the proportion of meadows increased at 1,000 m (Fig. 4e). Lepidopteran larval abundance was on average 2.4 times lower in landscapes with a greater proportion of meadows compared with landscapes with lower proportion of meadows. Moreover, neither parasitoid : host ratios nor lepidopteran larval abundance were affected by the proportion of cropland, seminatural areas, or habitat diversity at any scale (Fig. 3).

Plant damage was directly influenced by the proportion of meadows in the landscape in conflicting ways. There was a positive relationship between proportion of meadows and plant damage at 250 m, but the relationship was negative at 1,000 m. The proportion of cropland, seminatural habitats, and habitat diversity did not impact plant damage at any scale (Fig. 3). In contrast to plant damage, crop yield was not directly influenced by landscape composition at any scale. However, crop yield was negatively related with an increase in plant damage caused by insect injury (Fig. 5).

### *Path analysis to assess the direct and indirect relationships between landscape composition and crop yield*

Based on results of the previous sections, we parameterized the path model using proportion of meadows at 250 and 1,000 m as indicator of landscape composition. The results of Shipley's test of *d*-separation supported the causal assumptions in the path model indicating that they provided a good fit to the data (Fisher's $C = 13.03$, df = 18, $P = 0.790$). According to the best path model (Fig. 6), crop yield was not directly influenced by either landscape composition or pest

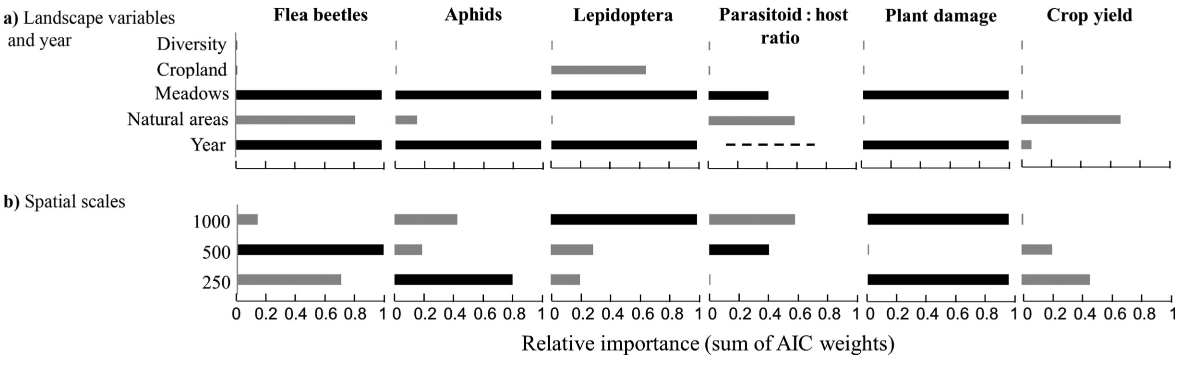

FIG. 3. (a) Relative importance of landscape variables and year of study in explaining insect pest abundance, parasitoid : host ratios, plant damage, and crop yield across spatial scales. We estimated the relative importance of each landscape variable and time of the year by summing the Akaike weights of all competing models ($\Delta AIC_c < 2$; where $AIC_c$ is the Akaike information criterion corrected for sample size) at all scales containing the variable. The relative importance is 1 if the variable is included in all competing models and 0 if the variable is not included in any of the models. Black bars indicate variables that were statistical significant ($P < 0.05$) based on a conditional *F* test (Pinheiro and Bates 2000; Appendix S1), while gray bars indicate no statistical significance. Dashed lines represent variables whose relative importance were not estimated because they were not included in the finals models. (b) Relative importance of each spatial scale in explaining insect pest abundance, parasitoid : host ratios, plant damage, and crop yield. Relative importance was calculated by summing the Akaike weights across all models in the set where a given scale appears. As previously, values closer to 1 indicate increased importance of a given spatial scale. Black bars indicate the most predictive scale for each variable (Appendix S1).

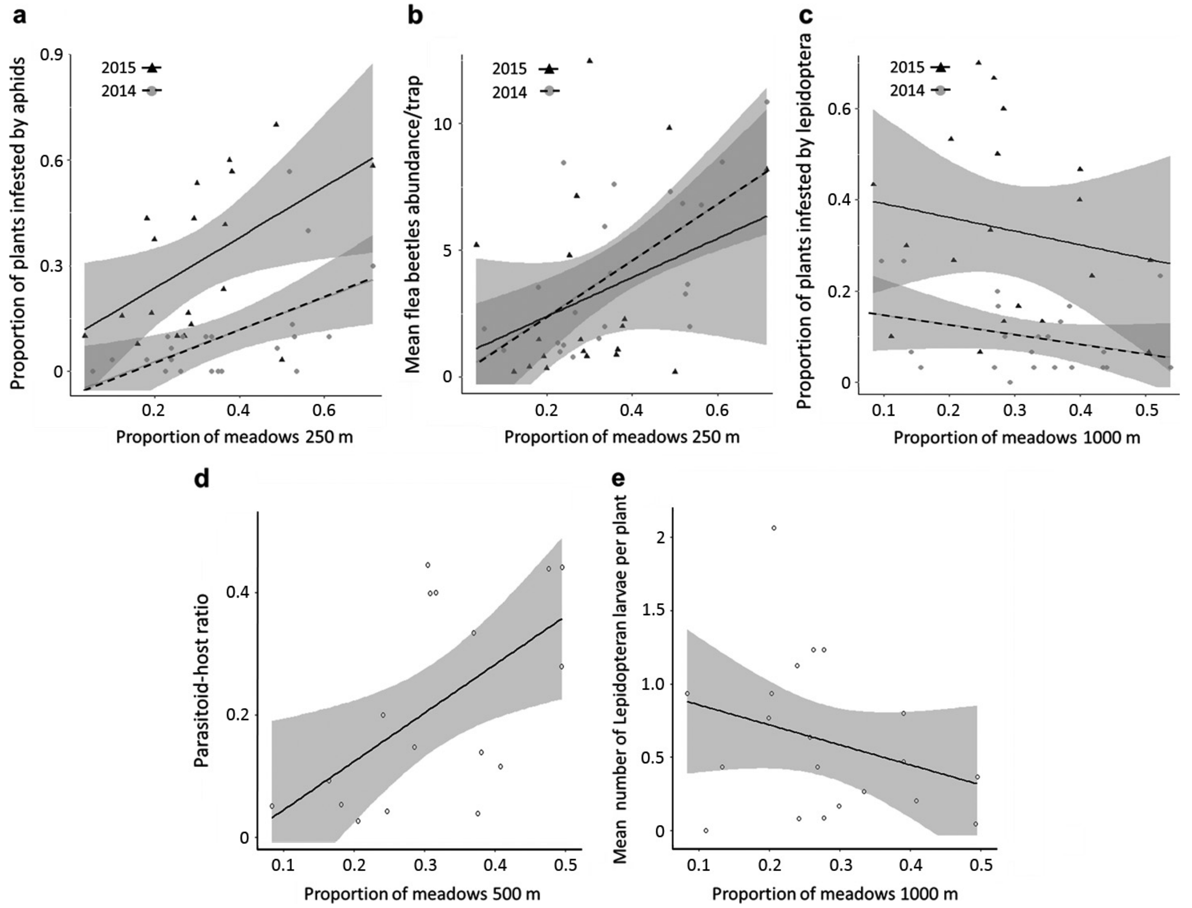

FIG. 4. Relationship between the proportion of meadows around the experimental fields and (a) aphid incidence (250 m radius), (b) flea beetle abundance (250 m radius), (c) Lepidoptera (i.e., *Pieris rapae*, *Plutella xylostella*, and *Trichoplusia ni*) incidence (1000 m radius), (d) parasitoid (*Cotesia rubecula*) : host (*Pieris rapae* larvae) ratios (500 m radius), and (e) mean number of *P. rapae* larvae per plant (1000 m radius). Lines are the fixed-effect predictions from the best models without covariables and associated 95% confidence intervals (gray shaded).

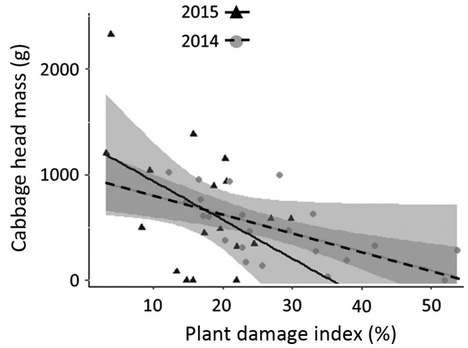

FIG. 5. Relationship between plant damage index (percentage of leaf area removed by herbivores) and cabbage yield (mean mass of marketable cabbage heads). Lines are the fixed-effect predictions from the best model without covariables and associated 95% confidence intervals (gray shaded).

incidence. However, landscape composition had an indirect effect on crop yield by affecting both pest incidence and plant damage (Table 1). Specifically, there was positive direct effect of the proportion of meadows at 250 m radius on flea beetle abundance, but negative direct effect of the proportion of meadows at 1,000 on Lepidoptera incidence. Likewise, there was a positive direct and indirect relationships between proportion of meadows and plant damage at 250 m, but the relationships were negative at 1,000 m (Table 1).

The path analysis also suggested that crop yield was indirectly influenced by the variability between years in pest incidence and plant damage (Fig. 6). Plant damage was mainly inflicted by flea beetles and Lepidopteran larvae that showed a remarkable variation in incidence between growing seasons. Overall, flea beetle incidence was higher in 2014 than in 2015, while the opposite pattern was observed for Lepidopteran incidence. As a result, there was also significant variability among years in plant damage, with higher mean values in 2014 compared with 2015 (2014, 28% ± 3%; 2015, 17% ± 2%). Although crop yield was on average lower in 2014 compared with 2015 (marketable head mass in 2014, 507 ± 68 g; 2015, 691 ± 124 g), there was no significant direct effect of year on crop yield (see Fig. 6).

## DISCUSSION

We expected that landscape simplification, through reduced diversity of land cover types and an increase in the proportion

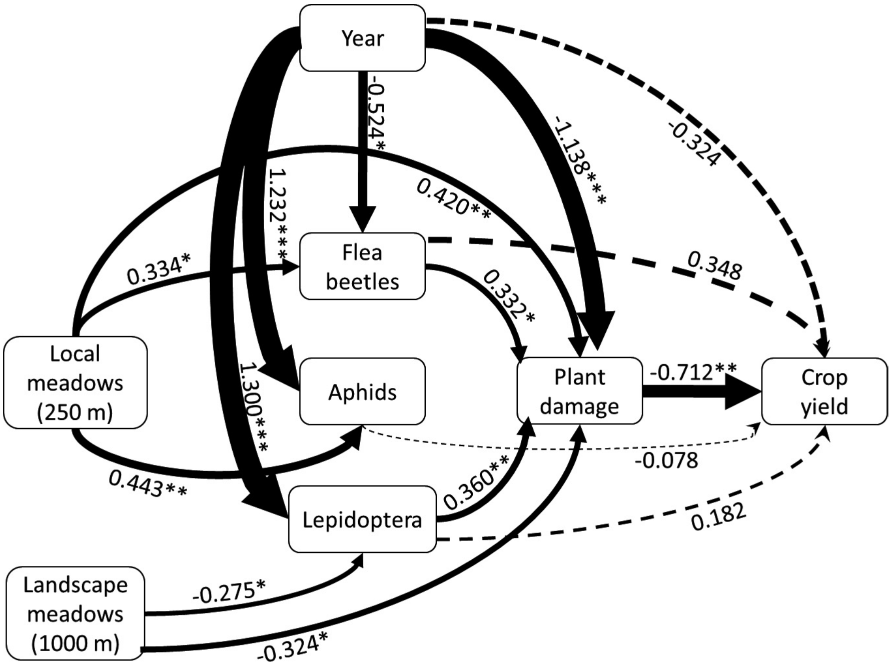

Fig. 6. Path model for relationships between landscape composition, year of study, pest incidence, pest abundance, plant damage, and crop yield. Solid lines indicate significant effects, while dashed lines denote nonsignificant effects. The number along the arrows are standardized path coefficients obtained from mixed effect models, and stars demark the significance level (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). The width of each arrow is proportional to the strength of the relationship.

Table 1. Relative strengths of the direct and indirect effects in the path model depicting the causal relationships between landscape composition, pest abundance, plant damage, and crop yield (Fig. 6).

| Response variable, predictor, and type of effect | Mediator variable | Standardized path coefficient |
|---|---|---|
| Plant damage | | |
| Local meadows | | |
| Direct | none | **0.502** |
| Indirect | flea beetles | **0.118** |
| Landscape meadows | | |
| Direct | none | **−0.359** |
| Indirect | Lepidoptera | **−0.120** |
| Crop yield | | |
| Flea beetles | | |
| Direct | none | 0.323 |
| Indirect | plant damage | **−0.075** |
| Lepidoptera | | |
| Direct | none | 1.286 |
| Indirect | plant damage | **−0.109** |
| Local meadows | | |
| Direct | none | −0.246 |
| Indirect | flea beetles | 0.230 |
| Indirect | plant damage | **−0.042** |
| Landscape meadows | | |
| Direct | none | −3.031 |
| Indirect | Lepidoptera | 1.219 |
| Indirect | plant damage | 0.153 |

*Notes:* Standardized path coefficients are shown, with corresponding statistical significance. Boldface text indicates significant relationships ($P < 0.05$).

of cropland over the landscape, would be positively correlated with pest abundance or incidence. Contrary to our initial hypothesis, pest abundance and pest incidence were neither influenced by the proportion of cropland nor the diversity of land cover types in the landscape. Rather, pest pressure in cabbage for all three herbivore taxa was best explained by the presence of uncultivated habitats surrounding the cabbage fields. Flea beetles and aphids were positively correlated with the proportion of meadows at 250 m, whereas lepidopteran incidence was negatively correlated with the proportion of meadows at a 1,000-m scale. Our analysis also revealed that landscape composition can indirectly influence crop yield via landscape-mediated effects on the abundance of both insect pests (i.e., flea beetles and lepidopteran larvae) and natural enemies (i.e., lepidopteran parasitoids).

Two non-mutually exclusive mechanisms could explain the lack of relationship between pest abundance and landscape simplification. First, pest survival may depend upon resources that might also occur in habitats other than croplands. In fact, this seems to be the most likely explanation for the positive association between the increasing area of meadows and the abundance of flea beetles and aphids. There is substantial evidence that meadows may serve as overwintering habitat and shelter for flea beetles and aphids (Andersen et al. 2005, Chaplin-Kramer et al. 2011a, Al Hassan et al. 2012). Furthermore, meadows may provide food resources that play a crucial role in favoring the survival and subsequent development of pest populations when cabbage is not grown. Adult flea beetles and aphids can feed on a wide variety of non-cultivated crucifer species that commonly occur in meadows near agricultural fields (e.g., *Barbarea vulgaris* R. Br., *Sinapis arvensis* L., and *Capsella bursa-pastoris* L.), thereby facilitating their survival year-round (Cole 1997, Mayoori and Mikunthan 2009, Chaplin-Kramer et al. 2011*a*). This suggests that the proportion of meadows around the farm might be more important than the total amount of cropland in determining pest pressure by flea beetles and aphids in the study region.

Second, pest populations are affected by the landscape not only directly, but also indirectly through landscape effects on its natural enemies. Specifically, lepidopteran incidence in our study was negatively influenced by the proportion of meadows. This may be due to a landscape-mediated increase in abundance and activity of its natural enemies, which in turn could have a positive effect on biocontrol (i.e., increased parasitoid : host ratio). Parasitoid populations may have been enhanced by meadows because these non-crop habitats are able to provide sources of nectar and alternative hosts (Jervis et al. 1993, Williams and Martinson 2000), or due to a reduction in the frequency of insecticide application and habitat disturbance associated with less intensified farming practices (Jonsson et al. 2012). Indeed, *C. rubecula* is known to forage for hosts predominantly in crop fields and uncultivated meadows (Benson et al. 2003) and the availability of sugar sources in the field is vital for its reproductive success (Siekmann et al. 2004). Furthermore, we found that lepidopteran densities were on average 2.4 times lower in landscapes with a greater proportion of meadows, indicating that lepidopterans are affected by landscape composition. Our results are in line with several studies demonstrating that increasing proportion of non-crop habitats at the landscape-scale can enhance biocontrol of lepidopteran pests by parasitoids in brassica fields (Bianchi et al. 2008, Jonsson et al. 2012, Letourneau et al. 2012).

It should be noted that meadows also had a direct effect on plant damage that is not entirely mediated by the species considered here (see Fig. 6, Table 1). It is possible that other natural enemies and pests may be driving these additional landscape effects on plant damage. For example, general predators can also play a significant role in controlling lepidopteran pests in brassica crops (Furlong et al. 2004, Bryant et al. 2014), which may be expected to lead to a reduction in plant damage. Likewise, other herbivores in the system (e.g., cabbage maggot) have the potential to cause considerable plant damage (Joseph and Martinez 2014). Importantly, some of these enemies and pests can also use non-crop habitats as refugia during disturbances caused by agricultural practices, causing them to recolonize crop fields from the surrounding landscape (Joseph and Martinez 2014, Saqib et al. 2017). Our data do not allow us to exactly determine which species may be driving these additional effects, but it highlights the importance of exploring landscape effects at multiple scales and across trophic levels. Clearly, disentangling the contribution of these unidentified drivers of plant damage warrants further study.

Taken together, our results reveal that meadows can provide resources that benefit both insect pests and biocontrol agents. Landscapes with a high proportion of meadows were associated with lower densities of *P. rapae* likely resulting from parasitism, but also with greater pest pressure by aphids and flea beetles, thereby counterbalancing potential benefits of biocontrol. Consequently, there is a trade-off between increasing the proportion of meadows to enhance biocontrol or decreasing it to reduce pest pressure. This finding agrees with previous studies (Bianchi et al. 2013), confirming that habitat patches in the same land-use class vary greatly in function over time and space creating the potential of counterbalancing effects for pest control. For example, Midega et al. (2014) found that grasslands provide habitat for lepidopteran stem borers and their parasitoids, but the net effect was an increase in stem borer density in landscapes with more grasslands. Similarly, pollen beetle densities and damage in oilseed rape were higher in fields surrounded by semi-natural habitats (Rusch et al. 2011, 2012), despite high levels of parasitism in these complex landscapes. From a plant protection perspective, the challenge is to identify landscape management strategies that selectively favor natural enemies over pests in a multi-pest species context. In this sense, this study suggested two important directions to improve our understanding of pest responses to landscape composition with respect to crop production.

First, our study highlights the importance of considering pest complexes rather than focusing on a single pest at a time when investigating the impact of landscape on pest management. By far, most landscape studies have evaluated impacts of landscape on a single pest species (reviewed by Bianchi et al. 2006, Veres et al. 2013), even though most agroecosystems support multiple pest and non-pest species. The combined effect of multiple herbivores may differ from the effects of each individual herbivore in a landscape, which may have implications for biocontrol (Fitzgerald and Jay 2013) and agricultural productivity (Dangles et al. 2009). Our results illustrate that enhancing pest suppression through landscape management is not a straightforward task, because the management of one pest species could lead to an increase in the abundance of another with cascading effects on crop yield. Furthermore, aphids and flea beetles were influenced by landscape composition at relatively finer spatial scales, whereas lepidopteran abundance was more responsive to a broader landscape scale. The complexities associated with the combined effects of multiple species and scales shown here provide a potential explanation for the lack of consistent effects of landscape composition on pest abundance and crop yield revealed by previous studies (Chaplin-Kramer et al. 2011*b*, Veres et al. 2013). Given these complexities, it is not surprising that, despite the large number of landscape pest control studies (Schellhorn et al. 2015), it has proven challenging to provide clear pest management recommendations to farmers. Thus, a more integrated understanding of the complex relationships between multiple species across trophic levels is required for guiding the implementation of feasible land-use practices in a way that is meaningful not only for managing a particular pest, but also for an overall net benefit on crop production.

Second, we suggest that future landscape studies need to consider the specific composition of plant species within suitable habitat patches, rather than using a rough land-cover classification. At the landscape scale, for example, the relative amount of a particular land cover type often does not capture the actual diversity of resources exploited by pests. For instance, flea beetles and aphids in our system may exploit a wide array of cruciferous weeds that can be scattered over the meadows. Likewise, floral resources in the meadows can provide habitat and complementary food sources for a wide variety of natural enemies including *C. rubecula*. Moreover, pest species like the imported cabbageworm, *P. rapae*, may exploit floral food sources as well (Winkler and Wa 2010), further confounding the patterns emerging between pest abundance and landscape composition. Therefore, the abundance of certain plant species, which occur at a relatively finer spatial scale, appears to constitute one of the most crucial features in predicting whether habitat patches have a positive or negative effect on pest control (Bahlai et al. 2010, Bianchi et al. 2013, Parry et al. 2015). Thus, studying the local floristic composition within specific habitat types in concert with landscape structure has the potential to provide more relevant data for effective pest management decisions.

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## Literature Cited

Al Hassan, D., F. Burel, M. Plantegenest, P. Kindlmann, A. Butet, and N. Parisey. 2012. Relationship between landscape composition and the abundance of aphids and their natural enemies in crop fields. Journal of Environmental Sciences 2:89–101.

Andaloro, J. T., K. B. Rose, A. M. Shelton, C. W. Hoy, and R. F. Becker. 1983. Cabbage growth stages. New York's Food and Life Sciences Bulletin 101. New York State Agricultural Experiment Station, Geneva, New York, USA.

Andersen, C. L., R. Hazzard, R. Van Driesche, and F. X. Mangan. 2005. Overwintering and seasonal patterns of feeding and reproduction in *Phyllotreta cruciferae* (Coleoptera : Chrysomelidae) in the northeastern United States. Environmental Entomology 34:794–800.

Bahlai, C. A., S. Sikkema, R. H. Hallett, J. Newman, and A. W. Schaafsma. 2010. Modeling distribution and abundance of soybean aphid in soybean fields using measurements from the surrounding landscape. Environmental Entomology 39:50–56.

Banks, J. E. 1998. The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. Oecologia 117:239–246.

Barton, K. 2015. MuMIn: Multi-model inference. R package version 1.15.1. Version 1:18. https://cran.r-project.org/web/packages/MuMIn/index.html.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Benson, J., R. G. Van Driesche, A. Pasquale, and J. Elkinton. 2003. Introduced braconid parasitoids and range reduction of a native butterfly in New England. Biological Control 28:197–213.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B 273:1715–1727.

Bianchi, F. J. J. A., P. W. Goedhart, and J. M. Baveco. 2008. Enhanced pest control in cabbage crops near forest in the Netherlands. Landscape Ecology 23:595–602.

Bianchi, F. J. J. A., N. A. Schellhorn, and S. A. Cunningham. 2013. Habitat functionality for the ecosystem service of pest control : reproduction and feeding sites of pests and natural enemies. Agricultural and Forest Entomology 15:12–23.

Bommarco, R., F. Miranda, H. Bylund, and C. Björkman. 2011. Insecticides suppress natural enemies and increase pest damage in cabbage. Journal of Economic Entomology 104:782–791.

Bowyer, R. T., J. G. Kie, D. K. Person, and K. L. Monteith. 2013. Metrics of predation: Perils of predator-prey ratios: Predator-prey ratios. Acta Theriologica 58:329–340.

Bryant, A., T. Coudron, D. Brainard, and Z. Szendrei. 2014. Cover crop mulches influence biological control of the imported cabbageworm (*Pieris rapae* L., Lepidoptera : Pieridae) in cabbage. Biological Control 73:75–83.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Page Springer, New York, New York, USA.

Chaplin-Kramer, R., and C. Kremen. 2012. Pest control experiments show benefits of complexity at landscape and local scales. Ecological Applications 22:1936–1948.

Chaplin-Kramer, R., D. J. Kliebenstein, A. Chiem, E. Morrill, N. J. Mills, and C. Kremen. 2011*a*. Chemically mediated tritrophic interactions: Opposing effects of glucosinolates on a specialist herbivore and its predators. Journal of Applied Ecology 48: 880–887.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011*b*. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14:922–932.

Cole, R. A. 1997. Comparison of feeding behaviour of two Brassica pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated brassica species. Entomologia Experimentalis et Applicata 85:135–143.

Dangles, O., V. Mesías, V. Crespo-Perez, and J. F. Silvain. 2009. Crop damage increases with pest species diversity: Evidence from potato tuber moths in the tropical Andes. Journal of Applied Ecology 46:1115–1121.

Dassou, A. G., and P. Tixier. 2016. Response of pest control by generalist predators to local-scale plant diversity: A meta-analysis. Ecology and Evolution 6:1143–1153.

Dray, S., and A. B. Dufour. 2007. The ade4 package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Fitzgerald, J., and C. Jay. 2013. Implications of alternative prey on biocontrol of pests by arthropod predators in strawberry. Biocontrol Science and Technology 23:448–464.

Furlong, M. J., Z. Shi, S. Liu, and M. P. Zalucki. 2004. Evaluation of the impact of natural enemies on *Plutella xylostella L.* (Lepidoptera : Yponomeutidae) populations on commercial Brassica farms. Agricultural and Forest Entomology 6:311–322.

Gardiner, A. M. M., D. A. Landis, C. Gratton, C. D. Difonzo, M. O. Neal, J. M. Chacon, T. Wayo, N. P. Schmidt, E. E. Mueller, and G. E. Heimpei. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. Ecological Applications 19:143–154.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.

Herlihy, A. M. V., et al. 2012. Distribution of *Cotesia rubecula* (Hymenoptera : Braconidae) and its displacement of *Cotesia glomerata* in Eastern North America. Florida Entomologist 95:461–467.

Hooks, C. R. R., and M. W. Johnson. 2003. Impact of agricultural diversification on the insect community of cruciferous crops. Crop Protection 22:223–238.

Jervis, M. A., N. A. C. Kidd, M. G. Fitton, T. Huddleston, and H. A. Dawah. 1993. Flower-visiting by hymenopteran parasitoids. Journal of Natural History 27:67–105.

Jonsson, M., H. L. Buckley, B. S. Case, S. D. Wratten, R. J. Hale, and R. K. Didham. 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. Journal of Applied Ecology 49:706–714.

Joseph, S. V., and J. Martinez. 2014. Incidence of cabbage maggot (Diptera: Anthomyiidae) infestation and plant damage in seeded

Brassica fields in California's central coast. Crop Protection 62:72–78.

Joshi, N. K., M. Otieno, E. G. Rajotte, S. J. Fleischer, and D. J. Biddinger. 2016. Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. Frontiers in Ecology and Evolution 4:38.

Karsten, H. D., and M. Carlassare. 2002. Describing the botanical composition of a mixed species Northeastern U.S. pasture rotationally grazed by cattle. Crop Science 42:882–889.

Letourneau, D. K., and B. Goldstein. 2001. Pest damage and arthropod community structure in organic vs. conventional tomato production in California. Journal of Applied Ecology 38: 557–570.

Letourneau, D. K., S. G. B. Allen, and J. O. Stireman. 2012. Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. Journal of Applied Ecology 49:1405–1416.

Liere, H., T. N. Kim, B. P. Werling, T. D. Meehan, D. A. Landis, and C. Gratton. 2015. Trophic cascades in agricultural landscapes: Indirect effects of landscape composition on crop yield. Ecological Applications 25:652–661.

Lim, G. S., A., Sivapragasum., and M. Ruwaida. 1986. Impact assessment of *Apanteles plutellae* on Diamondback moth using the insecticide-check method. Pages 195–204 *in* N. S. Talekar and T. D. Griggs, editors. Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Centre, Shanhau, Taiwan.

Martin, E., B. Reineking, B. Seo, and I. Steffan-Dewenter. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the National Academy of Sciences USA 110:5534–5539.

Martin, E. A., B. Seo, C.-R. Park, B. Reineking, and I. Steffan-Dewenter. 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecological Applications 26:448–462.

Mayoori, K., and G. Mikunthan. 2009. Damage pattern of cabbage flea beetle, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae) and its associated hosts of crops and weeds. American-Euroasian Journal of Agricultural and Environmental Sciences 6:303–307.

Midega, C. A. O., M. Jonsson, Z. R. Khan, and B. Ekbom. 2014. Effects of landscape complexity and habitat management on stemborer colonization, parasitism and damage to maize. Agriculture, Ecosystems and Environment 188:289–293.

Mohler, C. L. 1991. Plant community types of the central Finger Lakes Region of New York: a synopsis and key. Proceedings of the Rochester Academy of Sciences 17:55–107.

Montgomery, D. C., and E. A. Peck. 1992. Introduction to linear regression analysis. Second edition. John Wiley and Sons, New York, New York, USA.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Naranjo, S. E., and P. C. Ellsworth. 2009. Fifty years of the integrated control concept: Moving the model and implementation forward in Arizona. Pest Management Science 65:1267–1286.

O'Rourke, M. E., K. Rienzo-Stack, and A. G. Power. 2011. A multi-scale, landscape approach to predicting insect populations in agroecosystems. Ecological Applications 21:1782–1791.

Parry, H. R., S. Macfadyen, J. E. Hopkinson, F. J. J. A. Bianchi, M. P. Zalucki, A. Bourne, and N. A. Schellhorn. 2015. Plant composition modulates arthropod pest and predator abundance: Evidence for culling exotics and planting natives. Basic and Applied Ecology 16:531–543.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-Plus. Springer Verlag, New York, New York, USA.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package version 3.1-122 R package:1–3. https://cran.r-project.org/web/packages/nlme/index.html.

Poveda, K., E. Martínez, M. F. Kersch-Becker, M. A. Bonilla, and T. Tscharntke. 2012. Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. Journal of Applied Ecology 49:513–522.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rand, T. A., D. K. Waters, S. L. Blodgett, J. J. Knodel, and M. O. Harris. 2014. Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes. Agriculture, Ecosystems and Environment 186:135–143.

Rempel, R. S., D. Kaukinen, and A. P. Carr. 2012. Patch analyst and Patch grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Rijnhart, J., J. Twisk, M. Chinapaw, M. de Boerc, and M. Heymans. 2017. Comparison of methods for the analysis of relatively simple mediation models. Contemporary Clinical Trials Communications 7:130–135.

Rusch, A., M. Valantin-Morison, J. P. Sarthou, and J. Roger-Estrade. 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. Landscape Ecology 26:473–486.

Rusch, A., M. Valantin-Morison, J. Roger-Estrade, and J. P. Sarthou. 2012. Using landscape indicators to predict high pest infestations and successful natural pest control at the regional scale. Landscape and Urban Planning 105:62–73.

Rusch, A., et al. 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agriculture, Ecosystems and Environment 221:198–204.

Saqib, H. S. A., M. You, and G. M. Gurr. 2017. Multivariate ordination identifies vegetation types associated with spider conservation in brassica crops. Peer Journal 5:e3795.

Schellhorn, N. A., H. R. Parry, S. Macfadyen, Y. Wang, and M. P. Zalucki. 2015. Connecting scales: Achieving in-field pest control from areawide and landscape ecology studies. Insect Science 22:35–51.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Siekmann, G., M. A. Keller, B. Tenhumberg, G. Siekmann, M. A. Keller, and B. Tenhumberg. 2004. The sweet tooth of adult parasitoid *Cotesia rubecula* : Ignoring hosts for nectar? Journal of Insect Behavior 17:459–476.

Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. Science 285:893–895.

Thies, C., I. Roschewitz, and T. Tscharntke. 2005. The landscape context of cereal aphid – parasitoid interactions. Proceedings of the Royal Society B 272:203–210.

Tingley, D., T. Yamamoto, K. Hirose, L. Keele, and K. Imai. 2014. Mediation: R package for causal mediation analysis. Journal of Statistical Software 59:1–38.

Tscharntke, T., et al. 2016. When natural habitat fails to enhance biological pest control—five hypotheses. Biological Conservation 204:449–458.

USDA, National Agricultural Statistics Service. 2015. New York cropland data layer (2015 ed.). USDA-NASS, Washington, D.C, USA. https://nassgeodata.gmu.edu/CropScape/

Van Driesche, R. G. 2008. Biological control of *Pieris rapae* in New England: host suppression and displacement of *Cotesia glomerata* by *Cotesia rubecula* (Hymenoptera: Braconidae). Florida Entomologist 91:22–25.

Veres, A., S. Petit, C. Conord, and C. Lavigne. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agriculture, Ecosystems and Environment 166:110–117.

Werling, B. P., and C. Gratton. 2010. Local and broadscale landscape structure differentially impact predation of two potato pests. Ecological Applications 20:1114–1125.

Williams, L., and T. E. Martinson. 2000. Colonization of New York vineyards by *Anagrus* spp. (Hymenoptera: Mymaridae): overwintering biology, within-vineyard distribution of wasps, and parasitism of grape leafhopper, *Erythroneura* spp. (Homoptera: Cicadellidae), eggs. Biological Control 18:136–146.

Winkler, K., and F. L. Wa. 2010. Assessing risks and benefits of floral supplements in conservation biological control. BioControl 55:719–727.

Woltz, J. M., R. Isaacs, and D. A. Landis. 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agriculture, Ecosystems and Environment 152:40–49.

Zaller, J. G., D. Moser, T. Drapela, C. Schmöger, and T. Frank. 2008. Insect pests in winter oilseed rape affected by field and landscape characteristics. Basic and Applied Ecology 9:682–690.

## Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1695/full

## Data Availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.484tt