

LOCAL AND LANDSCAPE DRIVERS OF BIOLOGICAL PEST CONTROL
IN AGRICULTURAL SYSTEMS

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Biological insect pest control by natural enemies is an important component of sustainable crop production. To capitalize on the potential benefits of biological control, however, we need a clear understanding of the factors underpinning the biological and ecological relationships between pests and their natural enemies in agricultural landscapes. In my doctoral research, I explored how local and landscape composition influence the abundance, behaviors, and traits of insect pests and natural enemies, as well as the complex ecological interactions between them. Chapter 1 shows how different insect pest species within the same cropping system have contrasting responses to landscape composition, with some species having positive relationships with the proportion of non-crop habitats, while other species show the opposite response. Such contrasting responses create the potential for counterbalancing effects for pest control, where strategies to reduce one species may increase the abundance of another. Chapter 2 demonstrates that the effectiveness of augmentative releases of predators to enhance pest control is affected by the composition of the surrounding landscape. I found that increasing enemy abundance through augmentation may have net positive effects on pest control, but only in complex landscapes where habitat heterogeneity can create favorable conditions for complementarity between augmented and resident enemies. Chapter 3 focuses on the critical role of predator body size as a predictor of pest suppression. We found that communities with even representation of small and large-bodied species have greater pest control than communities dominated by either small or large-bodied predators. By influencing the body size distribution of predator communities, landscape composition consequently mediates the magnitude of pest suppression. Chapter 4 shows that landscape composition not only affects the consumptive, but

also non-consumptive effects of predators on prey. I demonstrated that pest populations from landscapes with higher predator abundance exhibited considerable reductions in plant feeding in response to the presence of predators alone. Importantly, such landscape-driven changes in predator abundance may lead to reduced plant feeding damage, even in the absence of actual predation. Overall, my research shows that agroecosystem management that aims to harness the benefits of biological control should consider a landscape perspective because processes governing pest suppression by natural enemies operate at scales greater than individual fields.

BIOGRAPHICAL SKETCH

Manuel Ricardo was born and raised in Bogotá, Colombia. He received a B.A. in Biology from the Universidad Nacional de Colombia, where he became interested in studying predator-prey interactions. Prior to arriving at Cornell, Manuel Ricardo worked at the Colombian Corporation of Agricultural Research on issues ranging from biological pest control to environmental evaluation of agricultural technologies. Since then, he has been interested in sustainable agriculture and the role of biodiversity in pest management. During his Ph.D., Manuel Ricardo studied how shifts in land-use patterns driven by agricultural intensification affect biodiversity and pest control services in agricultural landscapes.

Dedicated to
Marina for supporting me and always believing in me, and
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INTRODUCTION

Over the past 60 years, changes in farming practices associated with agricultural intensification have negatively affected the diversity and abundance of beneficial organisms in agricultural landscapes (Tschamntke et al. 2005). Beyond conservation considerations, this depletion of biodiversity is extremely troubling because it compromises the delivery of essential ecosystem services. For example, the decline in natural enemy diversity caused by landscape simplification in the Midwestern U.S. has reduced biological control services and consequently increased pesticide use at regional scales (Meehan et al. 2011). If agriculture is to meet the demands of a burgeoning human population, it will be necessary to understand how agricultural intensification affects biodiversity and the ecosystem services underpinning agricultural production.

This dissertation addresses these challenges from the perspective of biological pest control by natural enemies. Predators and parasitoids provide significant contributions to agricultural production by suppressing or reducing pest populations — a service estimated to be worth US\$4.5 billion annually in the U.S. alone — (Losey and Vaughan 2006). Yet, how to best promote biological control by natural enemies in agricultural fields remains a challenge. A great deal of attention has been given to reducing management intensity at the farm scale through decreasing agrochemical use or implementing habitat diversification practices — such as flower strips or hedgerows— to support populations of natural enemies. While implementing these on-farm strategies has successfully increased biocontrol in many instances (Jonsson et al. 2015), the actual efficacy is highly variable across geographies and cropping systems (Batáry et al. 2011). Recent studies exploring the ecological factors associated with such variable outcomes, have demonstrated that the effectiveness of local management strategies aimed at insect pest control depends strongly on the composition of the surrounding landscape (i.e., the relative proportions of crop and non-crop habitats in the landscapes surrounding crop fields) (Tschamntke et al. 2012).

Realizing the potential of biological pest control therefore requires a landscape perspective, because processes governing pest suppression by natural enemies operate at scales greater than individual fields (Tscharntke et al. 2007). For example, natural enemies may require complementary resources outside of individual crop fields such as nectar, pollen, alternative prey, and shelter for overwintering (Landis et al. 2000). Therefore, heterogeneous landscapes with a high proportion of non-crop habitats may support a greater abundance and diversity of natural enemies that then spill over into crop fields (Chaplin-Kramer et al. 2011). In turn, a more diverse community of natural enemies is expected to enhance pest suppression services and reduce crop damage (Rusch et al. 2016). Yet, a growing body of empirical research (e.g. Ricci et al. 2019) and modelling (Karp et al. 2018) has revealed that biological pest control also exhibits inconsistent responses to surrounding landscape composition. Indeed, increasing the proportion of non-crop habitat in the landscape may lead to positive, negative, or neutral consequences for pest suppression (Tscharntke et al. 2016, Karp et al. 2018). A better understanding of how different species respond to different scales of intensification (local and landscape) can move us from post hoc explanations of patterns, to an ability to predict the impacts of land-use changes on pest control provision. Here, I explored some of the underlying drivers explaining the variation in how insect pests, predators, predation rates, crop damage, and crop yields respond to landscape composition.

The majority of studies examining how insect pests respond to changes in landscape composition have focused on the responses of a single pest species. This 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. The lack of multiple-pest studies that examine both positive and negative effects of changes in landscape composition is a major impediment to advancing our understanding of how to design landscapes to optimize overall pest control. I address this knowledge gap in **chapter 1** by examining 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. Results indicated that landscape composition may have positive or negative effects depending on herbivore identity. Direct effects of landscape features or indirect effects mediated by natural enemies were identified as drivers of these contrasting responses. Indeed, I found a trade-off between increasing the proportion of non-crop habitats in the landscape to enhance biocontrol or decreasing it to reduce pest pressure, thereby creating the potential of counterbalancing effects for overall pest control. The study therefore adds further weight to the argument that greater focus must be placed on understanding the potential tradeoffs arising from the complex interactions among multiple pest and natural enemy species at landscape scales. This knowledge allows us to evaluate the effects of changes in landscape structure on pest control more thoroughly, and to guide future management decisions for an overall net benefit on crop production.

Landscape composition can also moderate the effectiveness of local management practices aimed at enhancing pest control. While previous studies have documented that landscape structure does indeed influence the effectiveness of local conservation biocontrol schemes (e.g., wildflower strips, Jonsson et al. 2015), it remains to be tested whether the landscape-dependency patterns of augmentative biocontrol are comparable to those observed with other local management practices. By combining field and lab experiments, **chapter 2** evaluated whether the effectiveness of augmentative releases of predators to enhance pest control and increase productivity in cabbage crops is affected by the composition of the surrounding landscape. I found that predator augmentation is effective in enhancing pest control in complex landscapes (i.e., landscapes containing a high proportion of natural habitats), but it can be either neutral or detrimental to pest control in simple landscapes (i.e., crop-dominated landscapes). Notably, landscape composition directly alters the strength of pest control by predators as well as induces trophic cascades with important yield consequences. This work thus has practical

implications for pest management practitioners as it provides a conceptual framework to predict when predator augmentation could strengthen or weaken pest suppression.

Chapter 3 expands on my previous empirical results by exploring the mechanisms contributing to positive relationships between predator diversity and natural pest suppression. I extended the analysis beyond predator species richness (i.e., the number of species) to focus on functional traits, such as predator body size, as drivers of pest control services across heterogeneous landscapes. I found that predator body size was positively related to pest suppression; however, the magnitude of this effect varied depending on the interactions between different sized predators. Thus, certain combinations of species can make predator communities perform better or worse in terms of biocontrol. Communities dominated by similar sized predators were associated with decreased biocontrol, while communities with even representation of small- and large-bodied species resulted in more effective pest control. As such, this study lends support to the notion that evenness within a single trait, body size, can promote predator complementarity and enhance pest control within realistic arthropod communities. Because landscape composition strongly influenced the body size distribution of co-existing predators, this study highlights that the landscape context should be considered if we are to accurately predict how changes in predator body size influence the outcome of predator-predator interactions and the emergent impacts on pest suppression.

Focusing on the Colorado potato beetle as a model system, I further explore in **chapter 4** how landscape-driven variation in predator abundance influenced the magnitude of behavioral responses of herbivores to predation risk. I showed that predator abundance was higher in agriculturally dominated landscapes (i.e., simple landscapes). Furthermore, herbivore populations from simple landscapes exhibited significantly higher levels of intra-clutch cannibalism and considerable reductions in plant feeding, behaviors known to reduce the likelihood of being predated. Together, these results provide the first empirical evidence of the occurrence of a ‘landscape of fear’ that shaped the magnitude of antipredator responses in an herbivorous insect. Even more importantly, our results suggest that such predator-induced

changes in herbivore behavior may lead to reduced plant feeding damage, even in the absence of actual predation. Results of this chapter highlight the need for a broader understanding of the range of mechanisms by which biological control could be strengthened in agricultural landscapes.

Collectively, these chapters provide important insights to guide the implementation of agricultural practices aimed at supporting pest control services and highlight the fact that achieving this can be difficult. A key message from these chapters is that the commonly held notion that increasing non-crop habitats in the landscape is always beneficial for biological control is misleading. Chapter 1 exemplifies how non-crop habitats may even provide sustenance for pests rather than natural enemies. Similarly, pest management recommendations based on the simplistic premise that increasing enemy abundance could enhance pest control, are likely to lead to unexpected, and sometimes unfavorable outcomes for pest control as presented in Chapter 2. Therefore, promoting the “right” kind of biodiversity (*sensu* Landis et al., 2000) is critical when seeking to use ecologically-based methods to promote pest control. Chapters 3 and 4 provide examples of such strategies. Moving beyond species richness, Chapter 3 suggests that agricultural practices that promote a predator assemblage with a diverse set of traits (i.e., body size) can provide benefits for pest control. Chapter 4 shows there is potential to manipulate non-consumptive effects for pest management. A recurring theme of these chapters is that the outcome of enhancing biodiversity in any particular system is modulated by the composition of the surrounding landscape. The following chapters detail the observed patterns in the relationship between landscape composition and biological pest control, and explore some of the underlying mechanisms that are responsible for these patterns.

REFERENCES

- Batáry, P., Báldi, A., Kleijn, D., and Tschamntke, T. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B*, 278: 1894–1902.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14: 922–932.
- Jonsson, M., Straub, C.S., Didham, R.K., Buckley, H.L., Case, B.S., Hale, R.J., Gratton, C., Wratten, S.D. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* **52**: 1274–1282.
- Karp, D.S. et al. 2018 Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *PNAS* 115: E7863–E7870.
- Landis, D.A., Wratten, S.D. and Gurr, G.M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175–201.
- Losey, J.E., and Vaughan, M. 2006. The economic value of ecological services provided by insects. *Bioscience* 56: 312–323.
- Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern U.S. *PNAS* 108:11500–11505.
- 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.
- Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J. C., Choisis, J.-P. et al. 2019. Local pesticide use intensity conditions landscape effects on biological pest control. *Proceedings of the Royal Society B* 286: 20182898.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., et al. 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agriculture, Ecosystems and Environment* 221:198–204.

- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., et al. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43: 294–309.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters* 8: 857–874.
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ... Westphal, C. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87: 661–685.
- Tscharntke, T. et al. 2016. When natural habitat fails to enhance biological pestcontrol—Five hypotheses. *Biological Conservation* 204: 449–458.

CHAPTER ONE

CONTRASTING EFFECTS OF LANDSCAPE COMPOSITION ON CROP YIELD MEDIATED BY SPECIALIST HERBIVORES

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 (Chaplin-Kramer and Kremen 2012, Dassou and Tixier 2016, Werling and Gratton 2010). 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 (Chaplin-Kramer and Kremen 2012, Gardiner et al. 2009), 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.

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. 2011b). 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 (Tschardt 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 Tschardtke 1999, Chaplin-Kramer et al. 2011b), we also hypothesized that (2) parasitoids would respond positively to the proportion of non-crop habitats in the landscape. And lastly, 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 brome grass, and white clover (Mohler 1991, Karsten and Carlsson 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, twenty-two experimental fields sites were sampled in 2014 and 22 other fields were sampled in 2015. Mean distance between experimental fields within a study area was 0.8 ± 0.3 km (mean \pm standard deviation), 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 S1.1). 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 and references therein) 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 1000 m radius (landscape scale). These scales were chosen because specialist insects respond strongly to landscape composition at these spatial extents (Chaplin-Kramer et al. 2011b). We found moderate correlations among some landscape variables (Appendix S1: table S1.2). However, collinearity among landscape predictors was examined, and there were no collinearity problems for any model. All landscape predictors included in the 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 Inc., Bellevue, WA, USA) in 128 cell plug trays (54 x 28 cm) and grown in the greenhouse. After seedling emergence, plants were watered every day and fertilized two times/week with an organic fish fertilizer 2-4-1(N-P-K) (Neptune's Harvest[®], Gloucester, MA, USA) for six weeks and then hardened off outside for 7 days prior to transplanting in the field. Plants were eight weeks old when the experiment began.

Within a year, each experimental field consisted of ten 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 5kg/100m² (Kreher's[®] composted poultry manure, Clarence, NY, 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, ten 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 ten 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 (see below for flea beetle abundance). Samples were collected four times during the season at the seedling, pre-cupping, 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 corp., Kalamazoo, MI, USA) with a mixture of water and a few drops of organic, odorless detergent (Dr. Bronner's Unscented Pure Castile Soap, Vista, CA, 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 hours each time. In addition to recording densities of flea beetles using pitfall traps in 2015, we also used yellow sticky cards (15 x 30 cm, BioQuip Products, Grand Rapids, MI, 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 (<http://cuic.entomology.cornell.edu>). 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 ten 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 $\geq 80\%$. 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 (AICc) values of the full models across scales (i.e., considering the AICc among all data sets). Models with the smallest AICc-values were considered to better fit the data (Burnham and Anderson 2002). For models with similar fits ($\Delta\text{AICc} < 2$), 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 S1.2, S1.3, and S1.4.

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 ($\Delta\text{AICc} < 2$) 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 S1.5). 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 non-significant

relationships were removed (pathways where $P > 0.05$), or significant relationships were added, and AIC values re-assessed (Grace 2006). Models with lower AIC values are considered 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 not 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 less than 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. xylostea* (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, 2098 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 mean incidences (\pm SE) of Lepidopteran larvae $16 \pm 5\%$, aphids $11 \pm 4\%$, and flea beetles $46 \pm 7\%$ in 2014. In 2015, the mean incidence of lepidopteran larvae and aphids across experimental fields was 28 ± 4 and $30 \pm 1\%$, respectively, which was 3-fold higher than in 2014. In contrast, flea beetle incidence in 2015 was on average 6-fold lower (average 7 ± 3) than in 2014 (Fig. 1.1).

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 $16 \pm 5\%$ at the seedling stage and then decreased to $7 \pm 3\%$ 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 ($18 \pm 6\%$) at the seedling stage, and then decreased ($5 \pm 1\%$) by the maturation stage. In 2015, the peak incidence of aphids ($60 \pm 7\%$) 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: $46 \pm 7\%$, and 2015: $17 \pm 6\%$), and then populations declined at the maturation stage (2014: $29 \pm 7\%$, 2015: $2 \pm 1\%$) (Fig. 1.1).

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. 1.2). Although there was great within-site variability, parasitoid abundance across experimental fields correlated with the average number of *P. rapae* larvae over the 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. 1.3). 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. 1.4a and b). At the 1000 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 1000 m (Fig. 1.4c), 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. 1.4d), whereas lepidopteran larval abundance decreased as the proportion of meadows increased at 1000 m (Fig. 1.4e). 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. 1.3).

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 1000 m. The proportion of cropland, seminatural habitats and habitat diversity did not impact plant damage at any scale (Fig. 1.3). 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. 1.5).

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 1000 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. 1.6) crop yield was not directly influenced by either landscape composition or pest incidence. However, landscape composition had an indirect effect on crop yield by affecting both pest incidence and plant damage (Table 1.1). 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 1000 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 1000 m (Table 1.1).

The path analysis also suggested that crop yield was indirectly influenced by the variability between years in pest incidence and plant damage (Fig. 1.6). 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 weight in 2014: 507 ± 68 g; 2015: 691 ± 124 g), there was no significant direct effect of year on crop yield (see Fig. 1.6).

Discussion

We expected that landscape simplification, through reduced diversity of land cover types and an increase in the proportion 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 1000m 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 over-wintering 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, Mayoore, K., Mikunthan 2009, Chaplin-Kramer et al. 2011a). 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, William 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 (Siekman 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. 1.6, Table 1.1). 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 (Bryant et al. 2014, Furlong et al. 2004), 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, Saquib 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. 2011b, 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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REFERENCES

- 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
- 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 1.9.13. Version 1:18.
- 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., 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.

- 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.
- 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 (3): 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, USA.
- Chaplin-Kramer, R., D. J. Kliebenstein, A. Chiem, E. Morrill, N. J. Mills, and C. Kremen. 2011a. 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., and C. Kremen. 2012. Pest control experiments show benefits of complexity at landscape and local scales. *Ecological Applications* 22:1936–1948.
- Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011b. 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.
- 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.
- 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.
- 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.
- Herlihy, A. M. V, R. G. Van Driesche, M. R. Abney, J. Brodeur, R. A. Casagrande, D. A. Delaney, T. E. Elkner, S. J. Fleischer, D. S. Gruner, J. P. Harmon, G. E. Heimpel, K. Hemady, T. P. Kuhar, A. M. Shelton, A. J. Seaman, M. Skinner, R. Weinzierl, K. V. Yeargan, and Z. Szendrei. 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.
- 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.
- 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., 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.
- 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., Sivapragasam, A., Ruwaida, M. 1986. Impact assessment of *Apanteles plutellae* on Diamondback moth using the insecticide-check method. In N.S. Talekar & T.D. Griggs (eds.). *Diamondback Moth Management: Proceedings of the First International*

- Workshop. Asian Vegetable Research and Development Centre, Shanhou, Taiwan.:195–204.
- 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.
- 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.
- Mayoori, K., Mikunthan, G. 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 & 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* (2nd ed), New York: John Wiley and Sons, Inc.504p.
- 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., D. Bates, S. DebRoy, D. Sarkar, and R. R Development Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package version 3.1-122 R package:1–3.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed effects models in S and S-Plus*. Springer VerlagNewYork:528.
- Poveda, K., E. Martínez, M. F. Kersch-Becker, M. A. Bonilla, and T. Tschardtke. 2012. Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. *Journal of Applied Ecology* 49:513–522.
- R Core Team. 2015. R Development Core Team. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.:URL <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, A.P Carr. 2012. *Patch analyst and Patch grid*. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- 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., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tschardtke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems and Environment* 221:198–204.

- 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., 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.
- Saqib H.S.A., M. You, and G. M. Gurr. 2017. Multivariate ordination identifies vegetation types associated with spider conservation in brassica crops. *PeerJ*. 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., I. Roschewitz, and T. Tschardtke. 2005. The landscape context of cereal aphid – parasitoid interactions. *Proceedings of the Royal Society B* 272:203–210.
- Thies, C., and T. Tschardtke. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893–895.
- 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
- Tschardtke, T., D. S. Karp, R. Chaplin-kramer, P. Batáry, F. Declerck, C. Gratton, L. Hunt, A. Ives, M. Jonsson, A. Larsen, E. A. Martin, A. Martínez-salinas, T. D. Meehan, M. O. Rourke, K. Poveda, J. A. Rosenheim, A. Rusch, N. Schellhorn, T. C. Wanger, S. Wratten, and W. Zhang. 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation* 204: 449-458.

- 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.

Table 1.1. 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. 1.6). Standardized path coefficients are shown, with corresponding statistical significance.

Response variable	Predictor	Type of effect	Mediator variable(s)	Standardized path coefficient¹
Plant damage	Local meadows	Direct	None	0.502
		Indirect	Flea beetles	0.118
Plant damage	Landscape meadows	Direct	None	-0.359
		Indirect	Lepidoptera	-0.120
Crop yield	Flea beetles	Direct	None	0.323
		Indirect	Plant damage	-0.075
Crop yield	Lepidoptera	Direct	None	1.286
		Indirect	Plant damage	-0.109
Crop yield	Local meadows	Direct	None	-0.246
		Indirect	Flea beetles	0.230
		Indirect	Plant damage	-0.042
Crop yield	Landscape meadows	Direct	None	-3.031
		Indirect	Lepidoptera	1.219
		Indirect	Plant damage	0.153

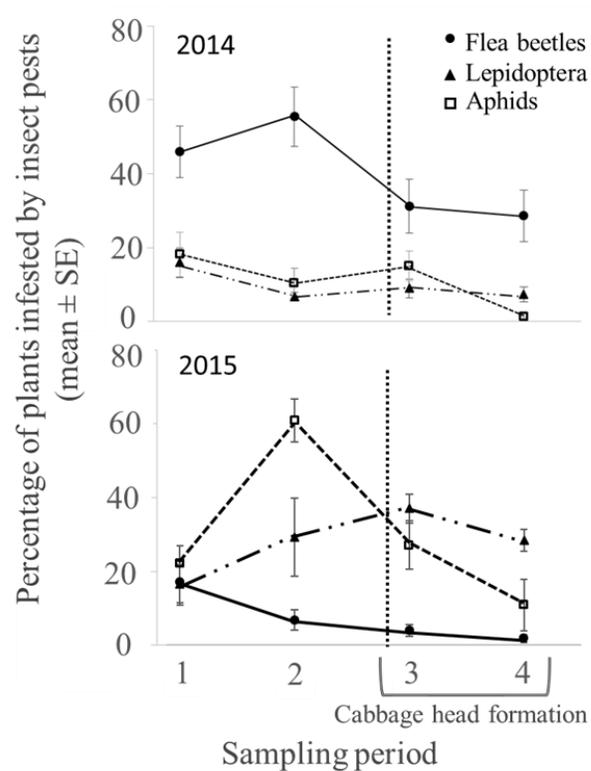


FIG. 1.1. Incidence (mean \pm SEM) of flea beetle adults, Lepidoptera larvae, and aphids across all experimental fields in 2014 and 2015. To determine incidence for each insect pest, 10 randomly selected cabbage plants per experimental field were visually inspected at 4 different times per year and the 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.

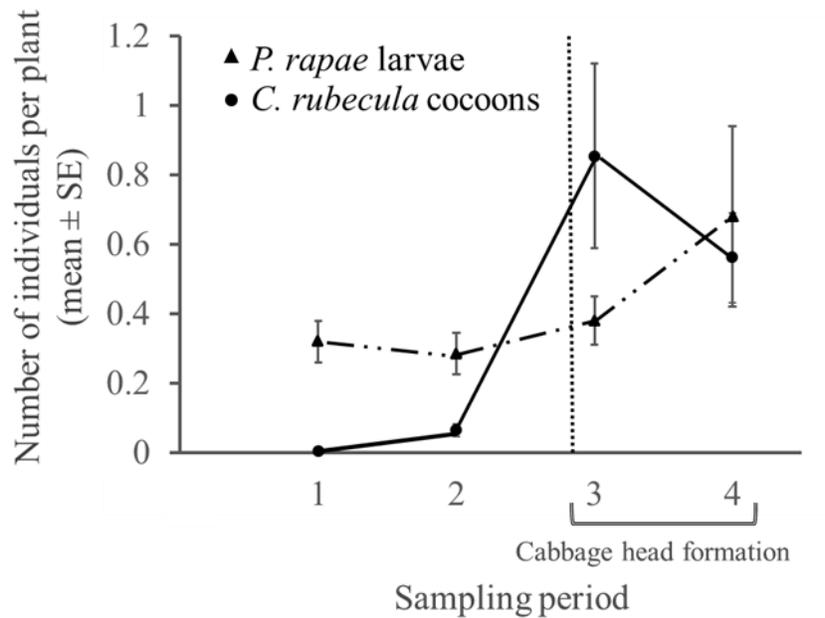


FIG. 1.2. Abundance (mean \pm SEM) of *Pieris rapae* larva and its parasitoid *Cotesia rubecula* on cabbage plants across all experimental fields. *P. rapae* larvae and *C. rubecula* were visually sampled on 10 randomly selected cabbage plants per experimental field at 4 sampling times during the growing season in 2015. Sampling occurred from late June to early September. Cabbage-head formation occurred between the third and fourth sampling periods.

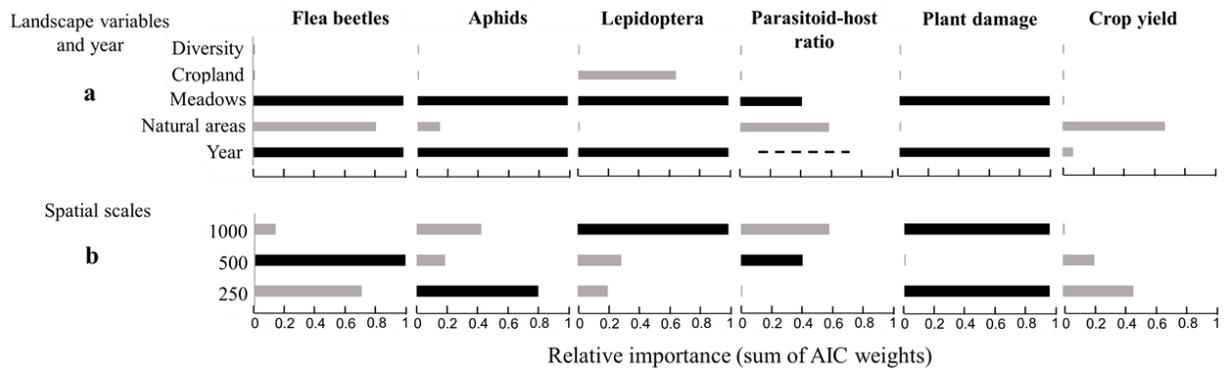


FIG. 1.3. (A) Relative importance of landscape variables and year of study in explaining insect pest abundance, parasitoid-host ratios, plant damage, and crop yield across spatial scales. We estimated the relative importance of each landscape variable and time of the year by summing the Akaike weights of all competing models ($\Delta AICc < 2$) 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 conditional F-test (Pinheiro and Bates 2000) (Appendix S1), while grey bars indicate no statistical significance. Dashed lines represent variables whose relative importance were not estimated because they were not included in the final 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).

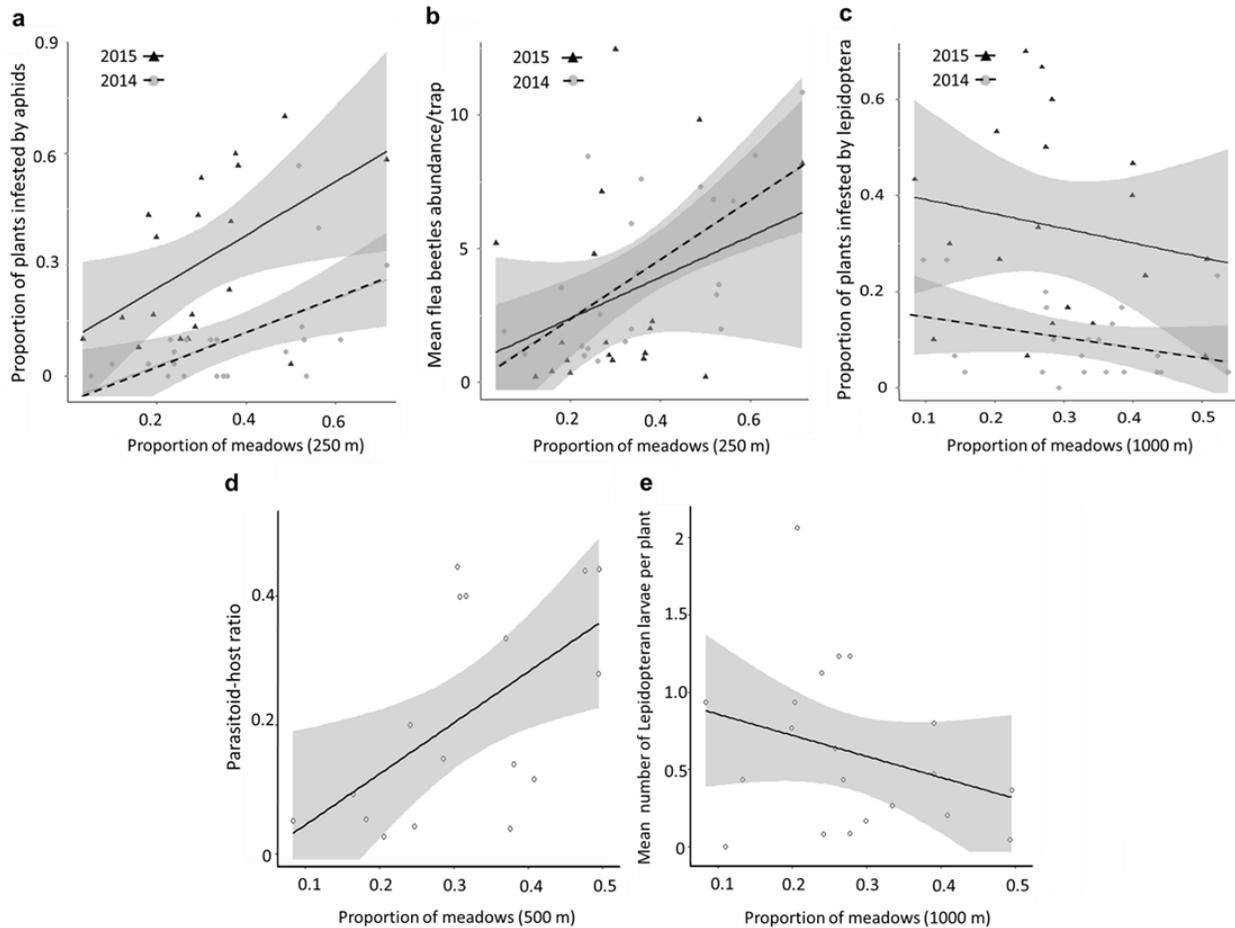


FIG. 1.4. Relationship between the proportion of meadows around the experimental fields and (a) aphid incidence, (b) flea beetle abundance, (c) lepidoptera (i.e. *Pieris rapae*, *Plutella xylostella* and *Trichoplusia ni*) incidence, (d) parasitoid (*Cotesia rubecula*)- host (*Pieris rapae* larvae)- ratios, and (e) mean number of *P. rapae* larvae per plant. Lines are the fixed-effect predictions from the best models without covariables and associated 95% confidence intervals (gray-shaded).

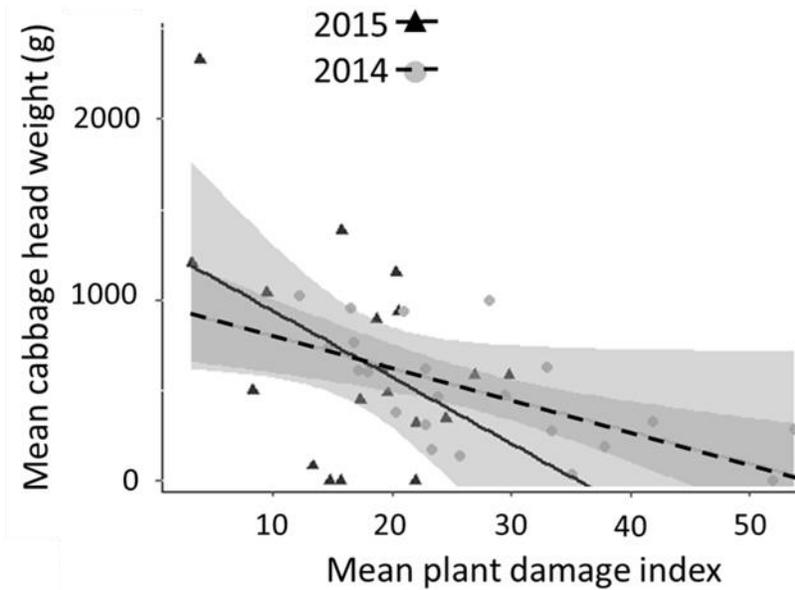


FIG. 1.5. Relationship between percentage of plant damage (proportion of leaf area removed by herbivores) and cabbage yield (mean weight of marketable cabbage heads). Lines are the fixed-effect predictions from the best model without covariables and associated 95% confidence intervals (gray-shaded).

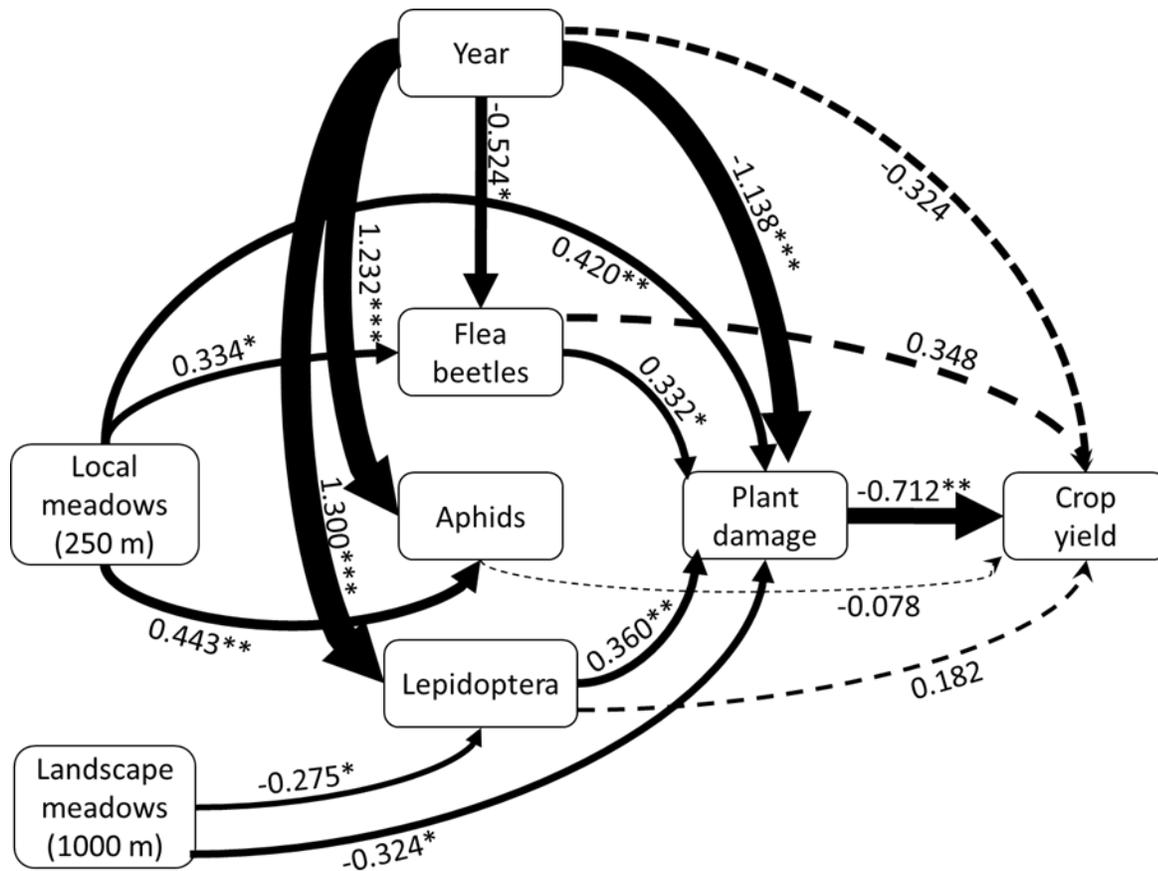


FIG. 1.6. Path model for relationships between landscape composition, year of study, pest incidence, pest abundance, plant damage, and crop yield. Solid lines indicate significant effects, while dashed lines denote non-significant effects. The number along the arrows are standardized path coefficients obtained from mixed effect models, and stars demark the significance level (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Width of each arrow is proportional to the strength of the relationship.

CHAPTER TWO
EFFECTIVENESS OF AUGMENTATIVE BIOLOGICAL CONTROL
DEPENDS ON LANDSCAPE CONTEXT

Abstract

Biological pest control by natural enemies is an important component of sustainable crop production. Among biological control approaches, natural enemy augmentation is an effective alternative when naturally occurring enemies are not sufficiently abundant or effective. However, it remains unknown whether the effectiveness of augmentative biocontrol varies along gradients of landscape composition, and how the interactions with resident enemies may modulate the collective impact on pest suppression. By combining field and lab experiments, we evaluated how landscape composition influenced the effectiveness of predator augmentation, and the consequences on pest abundance, plant damage, and crop biomass. We show for the first time that the effectiveness of predator augmentation is landscape-dependent. In complex landscapes, with less cropland area, predator augmentation increased predation rates, reduced pest abundance and plant damage, and increased crop biomass. By contrast, predator releases in simple landscapes had a negative effect on pest control, increasing plant damage and reducing crop biomass. Results from the lab experiment further suggested that landscape simplification can lead to greater interference among predators, causing a decrease in predator foraging efficiency. Our results indicate that landscape composition influences the effectiveness of augmentative biocontrol by modulating interactions between the introduced predators and the local enemy community.

Key words: *Brassica oleracea*; landscape complexity; multi-predator effects; natural enemies, *Pieris rapae*; pest control; predation; sustainable agriculture.

Introduction

Agricultural intensification is one of the main drivers of biodiversity loss and landscape simplification (Gómez-Virués et al. 2015). Intensive agricultural practices simplify the landscape by decreasing crop species diversity and transforming natural habitats into more agricultural land. These changes in land-use patterns not only directly affect the diversity and composition of arthropod species (Tscharrntke et al. 2005), but also potentially reduce the delivery of essential ecosystem services such as biological pest control (Landis et al. 2008). As a consequence, farming systems have become increasingly reliant on synthetic inputs, which in turn exacerbate the negative effects of intensified agriculture on the environment and biodiversity conservation (Meehan et al. 2011). In this context, there is a strong need to promote farming practices that harmonize agricultural production with the conservation and sustainable use of biodiversity (Scherr and McNeely 2008, Bommarco et al. 2013).

Biological pest control by natural enemies has thus become an important component for sustainable crop production (Bale et al. 2008). One strategy to improve biological control by resident natural enemies is enhancing habitat diversity through the provision of semi-natural vegetation in or around agricultural fields (Landis et al. 2000, Letourneau et al. 2011, Morandin et al. 2014). However, the most obvious potential disadvantage of these on-farm diversification strategies is that some land must be taken out of production, which may undermine any economic advantages gained through diversification (Letourneau et al. 2011, Blaauw and Isaacs 2014). Moreover, some of the benefits of habitat diversification may not manifest until a few years after implementation (Blaauw and Isaacs 2015, Morandin et al. 2016). These drawbacks may discourage farmers from adopting this approach, particularly for high-value crops. An alternative and potentially complementary avenue to enhancing biological control is the release of mass-reared natural enemies in large numbers to obtain an immediate control of pests. In fact, augmentative releases of natural enemies have proven to be an environmentally and

economically sound alternative to chemical pest control in a wide range of crop systems (van Lenteren 2012).

Yet, few studies, if any, have evaluated the effects of enemy augmentation on pest control when other naturally occurring enemies are already present in the system. Theoretically, natural enemy augmentation could improve pest control through niche complementarity or facilitation among natural enemies (Straub and Snyder 2012, Dainese et al. 2017). Alternatively, increasing enemy abundance could disrupt pest control through intraguild predation and/or behavioral interference (Finke and Denno 2005, Frank van Veen et al. 2006). Due to the complexity of ecological interactions among natural enemies, a predictive framework is lacking for when increasing enemy abundance will strengthen or weaken pest suppression. Considering the paucity of knowledge on this issue, we evaluated the interactions among augmented and resident enemies and how such interactions affected pest control.

While practitioners have often focused on implementing conservation biological control on a field-scale, empirical and theoretical work have shown that the effectiveness of these local strategies can depend on the composition of the surrounding landscape (Östman et al. 2001, Tschardt et al. 2005, 2012, Gabriel et al. 2010, Chaplin-Kramer and Kremen 2012). For instance, habitat diversification practices, such as implementing flower strips and hedgerows, are more effective for enhancing biocontrol in moderately simple landscapes (i.e., dominated by agricultural areas) than complex landscapes (i.e., containing a high proportion of semi-natural habitats) (Jonsson et al. 2015, Garratt et al. 2017). Results from recent meta-analysis also found that agro-environmental practices had the greatest positive effect on cropland diversity and associated ecosystem services in simple landscapes (Batáry et al. 2011, Scheper et al. 2013, Tuck et al. 2014). Like habitat diversification, the effectiveness of augmentative releases of natural enemies to improve pest control may depend on the composition of the surrounding landscape. However, it remains to be seen whether the landscape-dependency patterns of augmentative biocontrol are comparable to those observed with other local management practices.

Landscape composition could moderate augmentative biocontrol effects through two different mechanisms. First, as predators and parasitoids generally benefit from semi-natural habitats (Landis et al. 2000, Tschardt et al. 2007, but see Karp et al. 2018), increasing landscape complexity can increase resident enemy diversity and abundance (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). As a result, background levels of natural pest control can be sufficiently high in complex landscapes, making enemy augmentation ecologically redundant or even disruptive in this scenario (i.e., the intermediate landscape complexity hypothesis) (Tschardt et al. 2005, 2012, but see Concepción et al. 2008). Second, higher levels of habitat heterogeneity that characterize complex landscapes can have positive effects on the ability of multiple enemies to coexist due to the presence of additional non-pest prey and greater range of microhabitats (Janssen et al. 2007). By providing conditions that dampen antagonistic interactions among natural enemies, increasing landscape complexity may lead to a net positive impact of enemy augmentation (i.e., the habitat heterogeneity hypothesis) (MacArthur 1972). Both hypotheses have experimental support in a variety of systems (Finke and Denno 2002, Hughes and Grabowski 2006, Concepción et al. 2012, Jonsson et al. 2015); however, their validity for augmentative biocontrol practices remains unknown. Therefore, determining the landscape context under which enemy augmentation is likely to strengthen pest suppression is a key step towards developing ecologically-informed pest management strategies that benefit farmers. Furthermore, it is important to determine whether augmentative biocontrol might lead to cascading effects that influence plant performance (i.e., plant damage and crop biomass). Knowledge of crop productivity is important because this is the measure of biocontrol effectiveness of most relevance to growers, yet rarely quantified (but see Poveda et al. 2012, Liere et al. 2015, Grab et al. 2018).

We addressed these questions using the interaction between cabbage crops (*Brassica oleracea* L. var. *capitata*), the lepidopteran pest complex (*Pieris rapae*, *Plutella xylostella*, and *Trichoplusia ni*), and its natural enemies. The lepidopteran complex is one of the most destructive pests of brassica crops worldwide, with annual management costs estimated in the

billions of dollars (Ahuja et al. 2010, Philips et al. 2014). In central New York (USA), a diverse community of naturally occurring enemies composed of 156 predator species and 7 parasitoid species is associated with the three primary lepidopteran pests of cabbage (Schmaedick and Shelton 2000, Shelton et al. 2002). Among these natural enemies, two generalist predators have received considerable attention because they are common and relatively abundant in brassica crops in this region: the spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae), and the convergent ladybird beetle, *Hippodamia convergens* (Coleoptera: Coccinellidae) (B. Nault, personal observation). However, natural densities of these predators are generally unable to reduce pest populations below damaging levels (Schmaedick, M. 1999, Lundgren and Heimpel 2002), making augmentation of these commercially available predators a promising alternative to further increase the strength of pest suppression. *Podisus maculiventris* preferentially feeds on lepidopteran larvae, whereas *H. convergens* feeds mostly on lepidopteran eggs (Bryant et al. 2014). Such differential predation on particular stages of the same prey may lead to complementarity among predators, and ultimately enhance biological control.

Here, we conducted field and laboratory experiments to evaluate how landscape composition influenced the effectiveness of augmentative biocontrol of lepidopteran pests by *P. maculiventris* and *H. convergens*, and the subsequent effect on plant damage and crop biomass. Specifically, we asked: 1. Does augmentative biocontrol effectively enhance pest control and reduce plant damage?; 2. How does the interaction between landscape composition and enemy augmentation influence pest suppression?. We experimentally addressed these questions by releasing predators in cabbage fields situated in landscapes of varying complexity and evaluating whether predator augmentation suppressed pest populations to a greater extent than resident natural enemies acting alone. We further explored potential mechanisms responsible for our field results by evaluating the independent and combined effect of *P. maculiventris* and *H. convergens* on pest predation in the laboratory.

Materials and methods

Study region

The study was carried out from June to October 2015 in the Finger Lakes Region (42°26' N, 76°30' W) of New York State, USA. The landscape in this region is characterized by a mosaic of cropland and semi-natural habitats. Cropland in these landscapes mainly consisted of corn, soybean, winter wheat and crucifers, while semi-natural areas are composed of shrublands, woody wetlands, and mixed forest. We selected 11 farms across the study area to encompass a gradient of landscape complexity from landscapes with large amounts of semi-natural habitats (2% cropland) to simple landscapes dominated by crops (50% cropland) within a 1000 m radius around each farm. All farms selected for the study were either organic or used minimal inputs for pest management.

To quantify the landscape composition surrounding each farm, the proportion of semi-natural areas and cropland were calculated at three scales: 500 m, 1000 m, and 2000 m. These spatial scales are suitable for analyzing the effects of landscape context on pest control and natural enemies (Chaplin-Kramer and Kremen 2012). The landscape was characterized using the 2015 National Agricultural Statistics Service Cropland Data Layer for New York (USDA-NASS 2016) in ArcGIS 10.1.

Experimental plots

Seeds of fresh-market cabbage (*B. oleracea* var. capitata cv. Capture) were grown in an organic potting mix (sunshine®, Sun Gro Horticulture Inc., Bellevue, WA, USA), and fertilized with organic fish fertilizer 2-4-1(N-P-K) (Neptune's Harvest®, Gloucester, MA, USA) for seven weeks under greenhouse conditions. Plants were eight weeks old when they were transplanted to the field.

On each of the 11 farms, we established two experimental plots. One plot was randomly chosen for the augmentative predator release treatment while the other served as a non-release control. Plots within the same farm were separated by 334 ± 41 m (mean \pm 1 SE), and the mean distance between farms was 7.2 ± 2.3 km. Care was taken to minimize fine-scale landscape heterogeneity between experimental plots within the same farm. Plots within the same farm

primarily differed in the predator release treatment, while landscape context, plot size and shape, and abiotic conditions were similar for each pair.

Each experimental plot consisted of ten 7.2-m rows, with 15 cabbage plants per row. Row and plant spacing were 0.9 m and 0.45 m, respectively. Plants were transplanted across farms over two consecutive weeks in mid-June 2015. Experimental fields within the same farm were planted on the same day. Plants were fertilized during transplanting and again one month later using 8-3-3 (N-P-K) granular compost at a rate of 5kg/100m² (Kreher's® composted poultry manure, Clarence, NY, USA). All experimental plots were managed without fungicides or insecticides, and weeds were removed at two-week intervals.

Augmentative releases of predators

The predator release treatment included both *Podisus maculiventris* nymphs and *Hippodamia convergens* adults. Both the nymphal and adult stinkbugs display high predation rates on lepidopteran larvae, so we released fourth and fifth instars in our experiments to minimize dispersal after release and increase the potential for season-long pest control. Ladybird beetle larvae were not available commercially, which precluded us from using less-mobile stages. Predators were released three times throughout the season at the seedling, pre-cupping, and early head formation growth stages (Andaloro et al. 1983). Releases were conducted early in the season, as previous studies have shown that early control is key to the success of biocontrol strategies in field settings (Gardiner et al. 2009, Costamagna et al. 2015). Approximately 200 stinkbugs and 600 ladybeetles were released per plot each time by carefully deploying them on the leaves. These release rates equaled 1.3 sting bug nymph/plant and 4 ladybird adults/plant. These are commonly recommended release rates by commercial vendors (Cranshaw et al. 1996, A-1 Unique Insect Control 2017, Planet-Natural 2018, Rincon-Vitova 2018). No predators were released in the control plots.

P. maculiventris were obtained from eggs purchased from a commercial supplier (Beneficial Insectary Inc., Redding, CA, USA) and reared on a diet of mealworms, *Tenebrio molitor* (L.), and cabbage seedlings. The stinkbug colony was kept at $25.5 \pm 2.0^{\circ}\text{C}$, 60% RH, and

a photoperiod of 16:8 (L:D) following the methods of De Clercq et al. (1988). Adults of *H. convergens* were obtained from a commercial supplier (Arbico Organics, Oro Valley, AZ, USA). Ladybird beetles were stored at 7°C until we released them in the field.

Measuring predation rates in the field

Predation rates provided by resident and augmented predators were quantified using *Trichoplusia ni* larvae and eggs as sentinel prey. *Trichoplusia ni* were commercially available and easier to manipulate in field studies than *P. rapae*. *Trichoplusia ni* larvae and eggs were obtained from a commercial insectary (Benzon Research Inc., Carlisle, PA, USA). For estimating larval predation, 5 third-instars (13.6 ± 0.23 mm long) were placed on the upper leaves of four randomly selected plants per plot (i.e., 20 larvae per plot). After 24 h of exposure in the field, the remaining larvae were counted to determine the number of larvae consumed by predators. Larvae were considered predated if they were completely missing, or showed evidence of predation such as necrotic tissue around an open wound.

To estimate egg predation per plot, paper discs containing approximately 30 *T.ni* eggs (range: 19–76) were fixed to the underside of 10 x 10 cm pieces of corrugated plastic board (Coroplast®, Vanceburg, KY, USA) that provided a standardized foraging platform for predators. Five egg platforms were positioned at crop height and placed between the leaves of the plants where sentinel larvae were deployed. All egg masses were inspected after 24 h, and the number of eggs remaining were counted to determine predation rates. Eggs were considered predated if they were missing, the chorion presented clear evidence of attack (i.e., chewing predator), or the contents of the egg had vanished (i.e., attacks by a piercing-sucking predator). To distinguish sentinel prey predation from unknown losses due to handling and rainfall, we enclosed one plant per site in a cage that excluded natural enemies. Cages consisted of a 0.2 x 0.2 x 0.2 m³ mesh plastic screen (BioQuip, Rancho Dominguez, CA, USA) with openings of 1.1 x 0.7 mm², and whose bottom edges were buried 5 cm into the ground. Plants in these cages were infested with sentinel prey in the same fashion as the uncaged plants. Net mortality due to

predation was determined by assessing mortality from uncaged plants and subtracting it from mortality from caged plants.

We repeated the sentinel prey experiment three times per plot at the seedling, pre-cupping, and early head formation growth stages. Thus, we had three temporally separated dates that allowed us to account for the temporal differences in predation rates throughout the season.

Sampling of lepidopteran pests and their natural enemies

To assess lepidopteran abundance, plants were visually inspected for larvae during the seedling, pre-cupping, early head formation, and maturation growth stages (Andaloro et al. 1983). In each plot, ten randomly selected plants were destructively sampled and the number of larvae were recorded on each plant. To avoid possible edge effects, plants within 1 m of the edge of the plot were not sampled. A total of 294 caterpillars were collected in the experimental plots, with *P. rapae* as the dominant species (94% of the total caterpillars collected) followed by *P. xylostea* (5%) and *T. ni* (0.4%).

Naturally occurring predators and parasitoids were sampled using yellow sticky cards, pitfall traps, and visually inspected plants. Natural enemies from these samples were categorized into functional groups as foliar-foraging predators, ground-dwelling predators, and parasitoids. Our analysis was restricted to species known to attack either lepidopteran eggs or larvae based on previous observational and experimental studies (e.g., Schmaedick and Shelton 2000, Szendrei et al. 2014). For foliar-foraging predators, we focused on the three dominant species of coccinellids in our system: the native *Coleomegilla maculata* and the two-exotic species, *Harmonia axyridis* and *Propylea quatuordecimpunctata*. Abundance of all three coccinellid species were pooled to obtain the overall abundance of relevant foliar-foraging predators for each plot. For ground-dwelling predators, carabid beetles were collected and identified to species. Following identification, we gathered information from the literature to further classify carabids into three diet categories: carnivorous, omnivorous or phytophagous (Bousquet 2010, Homburg et al. 2013). Only carnivorous species were kept in further analyses. Altogether 25 predatory carabid species were collected, of which three species (*Bembidion quadrimaculatum*,

Poecilus chalcites and *Poecilus lucublandus*) made up 66% of the total capture. As with coccinellids, the abundance of predatory carabids for each plot was pooled in subsequent analysis. Lastly, we measured parasitoid abundance by focusing our sample efforts on *Cotesia rubecula* (Hymenoptera: Braconidae), the most important specialist parasitoid of *P. rapae* larvae in the study region (Herlihy et al. 2012). The parasitoids of the *T. ni* and *P. xylostella* were not investigated because both pests occurred in small numbers in our system (i.e. < 6% of the total caterpillars collected).

Sampling for all natural enemies was conducted three times during the season at the seedling, pre-cupping, and early head formation stages. Foliar-foraging predators, ground-dwelling predators and parasitoids were sampled using sticky cards, pitfall traps and visual inspection of plants, respectively. On each sampling time, one sticky card (15 x 30 cm, BioQuip, Rancho Dominguez, CA, USA) was positioned at crop height in the center of each plot. The sticky cards were retrieved after 15 days and the number of foliar-foraging predators were recorded. For the pitfall traps, a 540 mL clear plastic cup (9 cm diameter openings, Fabri-kal corp., Kalamazoo, MI, USA), was filled with a mixture of water and a few drops of organic, odorless detergent (Dr. Bronner's Unscented Pure Castile Soap, Vista, CA, 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 plot. Each trap was protected from rain and direct sunlight by a plastic plate (15 cm in diameter) held approximately 10 cm above the trap. Pitfall traps were collected after 24 h and the number of ground-dwelling predators was recorded. Finally, on each sampling date, parasitoid abundance was estimated by counting the total number of parasitoid cocoons (i.e, pupa) on ten randomly selected plants per experimental plot. Parasitoids were identified using diagnostic morphological characters described by Van Driesche (2008).

Plant damage and crop biomass

Insect damage and crop biomass were assessed from the same ten plants used for lepidopteran censuses at four sampling times during the season. 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 eight categories based on the percentage of leaf area removed: 0, 5-10, 10-20, 20-40, 40-60, 60-80, 80-100, or 100%). Visual estimates of damage provide the fastest and most cost-effective method for quantifying herbivory (Johnson et al. 2016), and previous studies have shown they can be precise and accurate to estimate economic thresholds for lepidopteran defoliation in cabbage (Chalfant et al. 1979). For analysis, we assumed the estimated proportion of damage on each plant to be the median of each category (0, 7, 15, 30, 50, 70, 90, 100, respectively). Crop biomass was determined by weighing the plants after they had been oven-dried at 60 °C for 7 days. Although the crop biomass at the end of the season (i.e. maturation growth stage) is a measure of crop yield (i.e. marketable cabbage head weight), we used the crop biomass throughout the season in our analyses rather than only final biomass, as the former allowed us to account for the temporal differences in the effectiveness of augmentative biocontrol. Analysis using only final crop yield produced qualitative similar results (Appendix S2: Fig. S2.1).

Laboratory experiment

Controlled lab experiments were conducted to quantify the individual and combined effect of stinkbugs and ladybird beetles on pest predation, independently from the effects of landscape context. Experimental units were 28×28×28 cm cages, covered on all sides, except the bottom, with a mesh screen opening of 1.1 x 0.7mm (BioQuip, Rancho Dominguez, CA, USA). Each experimental unit consisted of a single potted cabbage plant (*B. oleracea* var. capitata cv. Capture) with six fully-expanded true leaves. To begin the experiment, all cages received 5 third-instar larvae and one egg mass (approximately 30 eggs) in the same fashion as the sentinel field experiment. *T. ni* larvae were allowed to establish for 1 h before predator introduction.

Predators were released into individual cages according to four treatments: control (no predators added), stinkbug treatment (2 fifth-instars added), ladybird beetle treatment (5 adults added), and the interaction treatment (2 fifth-instar stinkbugs and 5 ladybird beetles adults added). These densities were chosen because they mimicked those used in the sentinel field

experiment. Each treatment was replicated eight times. The experiment had an additive design (i.e., overall predator density is higher in the multi-species treatment compared to the single-predator treatment), because this approach better reflects the effect of predator augmentation. Predators were starved for 24 h before being introduced to standardize hunger levels across treatments and then allowed to feed for an additional 24 h, after which the number of larvae and eggs remaining in the cages were recorded. The experiments were conducted at 25 ± 2 °C, $60 \pm 5\%$ RH and a 14:10 (L:D) h photoperiod.

Statistical analysis

To analyze the direct effect of the abundance of naturally occurring enemies on biocontrol of sentinel prey, pest incidence, and plant damage, we used linear mixed-effect models in R with the nlme package (Pinheiro et al. 2015). Abundances were averaged for each functional group separately (i.e. foliar-foraging predators, ground-dwelling predators, and parasitoids) and for each sampling period. Response variables were square-root-transformed to meet assumptions of normality and homoscedasticity (Zuur et al. 2009). For all models, we also included farm as random effect to account for other potential sources of variability associated with each geographic location (e.g., environmental or management intensity differences). Statistical significance of the abundance of each functional group was assessed by conditional *F*-tests (Pinheiro and Bates 2000).

The effects of landscape complexity and potential interactions with predator releases, on lepidopteran pest abundance, natural enemy abundance, predation rates, plant damage, and crop biomass, were examined using linear (lmer) and generalized linear mixed-effect models (glmer) (Bates et al. 2015). Fixed factors in the models included treatment (with or without predator releases), landscape complexity, and the treatment by landscape interaction. Landscape complexity was defined as either the proportion of cropland or the proportion of semi-natural areas as both variables were highly correlated at all scales (Spearman's $r_s < -0.45$, $P < 0.001$ at all scales). Random effects in all models included farm and sampling time to account for the crossed experimental design (i.e., each plot was measured on multiple dates and multiple plots were

measured on each date). Response variables were square-root transformed prior to analysis to meet normality assumptions and avoid heteroscedasticity. Assumptions were checked according to the graphical validation procedures recommended by Zuur et al. (2009). Models for foliar-foraging predators did not meet distributional assumptions, and therefore were analyzed using a generalized linear mixed model with a Poisson error distribution. Model simplification was done using a backwards-stepwise selection (lmer) or likelihood ratio tests (glmer) based on Akaike's Information Criterion (AIC) where non-significant predictors were removed ($P > 0.05$). We assessed the statistical significance of fixed effects and interaction terms by F-tests based on the Satterthwaite approximation (lmer) or Wald Z-test (glmer) (Kuznetsova et al. 2017, Luke 2017). Separate models were fitted for each landscape scale (i.e., 500, 1000, and 2000 m), and the scale with the highest explanatory power for each response variable was determined by comparing the AIC values of the minimum adequate models (Burnham and Anderson 2002). The most predictive scale for each response variable was then used in further analyses. Subsets of best models for each response variable are provided in Appendix S2: Table S2.1. Mantel test (Dray and Dufour 2007) indicated no spatial autocorrelation in the residuals of the final models (Appendix S2: Table S2.2).

To better understand potential differences between the predator release treatment and the control, we used the final models to estimate the marginal means and 95% confidence intervals for each response variable with the “emmeans” package in R (Lenth, R., Singmann H., Love J., Buerkner P. 2018). For all response variables (i.e., lepidopteran abundance, predation rates, plant damage, crop biomass, and natural enemy abundance), we used preplanned contrast to determine whether mean differences between plots with and without predator releases (i.e, effect size) were significant. We first estimated the mean effect size across the entire landscape complexity gradient to get an overall quantitative assessment of the consequences of predator augmentation for each response variable. In a second group of comparisons, we estimated the effect size of each response at even intervals over the landscape complexity gradient (range: 0-0.6) to test the hypothesis that the effects of augmented predators were contingent on the characteristics of the

surrounding landscape. Pairwise multiple comparisons were calculated using the Bonferroni correction for an overall error rate of 0.05. Comparisons were conducted using the emmeans package.

For the laboratory experiment, we examined predation rates on lepidopteran larvae and eggs using a two-way ANOVA followed by a Tukey HSD test at $P < 0.05$ including the factors: stinkbugs (with or without), ladybird beetles (with or without), and their interaction. Predation rates were log-transformed to meet the assumptions of the analysis. To further examine these data, we used a multiplicative risk model (Sih et al. 1998) followed by ANOVA comparing the expected and actual predation rate values to assess whether combined predators act independently (i.e., observed and predicted values do not differ, so that its combined effect is additive), antagonistically (i.e., observed values are less than the predicted values), or synergistically (i.e., observed values exceed the predicted values) on prey populations (Herrick et al. 2008). All statistical analyses were done using R v. 3.2.3 (Team 2015).

Results

Relationship between the abundance of naturally occurring enemies and pest control

Predation on sentinel eggs was significantly associated with the abundance of foliar-foraging predators ($F_{1,45} = 5.79$, $P = 0.020$), whereas neither ground-dwelling predators ($F_{1,46} = 0.578$, $P = 0.451$) nor parasitoids ($F_{1,46} = 1.166$, $P = 0.286$) were significantly correlated with egg predation. In contrast to egg predation, larval predation did not correlate significantly with the abundance of foliar-foraging predators ($F_{1,47} = 2.73$, $P = 0.105$). Rather, larval predation was positively correlated with the total abundance of ground-dwelling predators ($F_{1,51} = 22.02$, $P < 0.001$), but negatively related to parasitoid abundance ($F_{1,48} = 22.21$, $P < 0.001$) (Fig. 2.1).

The natural incidence of *P. rapae* larvae was not influenced by either foliar-foraging ($F_{1,43} = 0.435$, $P = 0.513$) or ground-dwelling predators ($F_{1,47} = 0.075$, $P = 0.785$). However, there was a positive relationship between the abundance of *P. rapae* larvae and parasitoid abundance ($F_{1,44} = 6.273$, $P = 0.016$), suggesting that parasitoids were positively host density-dependent. Finally, plant damage was negatively influenced by the abundance of ground-dwelling predators

($F_{1,51} = 9.134$, $P = 0.004$), but positively correlated with parasitoid abundance ($F_{1,48} = 11.55$, $P = 0.001$). Foliar-foraging predators, on the other hand, had no effect on plant damage ($F_{1,47} = 1.389$, $P = 0.245$) (Fig. 2.1).

Overall effects of augmentative predator releases

Augmentative releases of predators led to higher larval predation, lower plant damage, and higher crop biomass than the non-augmented control (Fig. 2.2, Table 2.1). Larval predation was 47% greater in the predator release treatment than in the control ($t = 2.04$, $P = 0.047$). Although larval predation was greater in the predator release treatment than in the control, we did not find differences in the mean abundance of naturally occurring caterpillars among treatments ($t = -1.49$, $P = 0.137$). Mean overall egg predation also did not differ significantly among predator and control plots ($t = -0.27$, $P = 0.788$). Lastly, no significant predator release effects were found for the overall abundance of any of the resident natural enemy groups (foliar-foraging: $z = -0.37$, $P = 0.711$; ground-dwelling: $t = -0.03$, $P = 0.974$; parasitoids: $t = -0.54$, $P = 0.587$).

Mean overall plant damage, estimated across the landscape complexity gradient, was reduced by 16% in the predator release plots relative to control plots ($t = -2.28$, $P = 0.023$). Importantly, average damage levels over the season were significantly correlated with the mean abundance of lepidopteran larvae (Pearson's $r = 0.33$, $P = 0.002$), confirming that leaf-chewing caterpillars were largely responsible for the foliar damage observed in our field study. Moreover, overall crop biomass was 26% higher in the predator release plots compared with the control ($t = 2.06$, $P = 0.040$). Crop biomass was negatively correlated with plant damage such that plots with greater plant damage had overall lower crop biomass (Pearson's $r = -0.48$, $P = 0.033$).

Interactions with landscape composition

Local effects of predator releases on larval predation were influenced by the composition of the surrounding landscape (Fig. 2.3, Table 1). The abundance of lepidopteran larvae was significantly influenced by the interactive effect of predator releases and the proportion of cropland at the 1000-m scale ($F = 4.80$, $P = 0.034$; Fig. 2.3a). Similarly, plant damage and crop

biomass were significantly influenced by the interactive effect of predator releases and the proportion of cropland at the 2000-m scale (plant damage: $F = 23.08$, $P < 0.001$; crop biomass: $F = 10.98$, $P = 0.002$; Figs. 2.3b & c). While caterpillar abundance and plant damage were significantly lower in the predator release treatment relative to the control in structurally complex landscapes (i.e., $< 20\%$ cropland), this tendency was reversed in cropland-dominated landscapes (i.e., $>40\%$ cropland) (Figs. 2.3d & e). Crop biomass was also similarly affected by landscape composition with greater biomass in predator release treatments relative to control plots in complex landscapes, but in simple landscapes the opposite trend was observed (Fig. 2.3f).

The interaction between predator releases and landscape composition did not significantly affect predation of sentinel larvae ($F = 0.02$, $P = 0.896$; Fig. 2.4a, Table 2.1). As a result, larval predation was consistently higher in predator release plots irrespective of the landscape context (Fig. 2.4c). In contrast, egg predation was modulated by the interaction between predator releases and the proportion of semi-natural areas at the 2000-m scale ($F = 4.62$, $P = 0.041$; Fig. 2.4b). Predator releases increased egg predation in complex landscapes, but had no effect in simple landscapes (Fig. 2.4d).

Landscape composition also had strong effects on resident natural enemy abundance. Foliar-foraging predator abundance was best predicted by the interaction between predator releases and the proportion of semi-natural areas at the 500-m scale ($z = 4.82$, $P < 0.001$; Fig. 2.5a). Predator releases reduced the abundance of foliar-foraging predators in simple landscapes, but increased the abundance in complex landscapes (Fig. 2.5d). The activity of ground-dwelling predators was positively related to the proportion of cropland at 2000-m scale ($F = 7.17$, $P = 0.021$; Fig. 2.5b), but no difference was detected between predator release and control plots across the landscape gradient (Fig. 2.5e). Parasitoid abundance was influenced by the interactive effect of predator releases and the proportion of semi-natural areas at the 1000-m scale ($F = 4.70$, $P = 0.037$; Fig. 2.5c). However, contrary to foliar-foraging predators, predator releases had an

adverse effect on parasitoid abundance in complex landscapes, but no effect in simple landscapes (Fig. 2.5f).

Interaction between stinkbugs and ladybird beetles in the laboratory

The outcome of the interaction between stinkbugs and ladybird beetles on prey predation depended on the developmental stage of the prey. Larval predation was greater in the stinkbug-only treatment (28%) than in the ladybird beetle-only treatment (5%), indicating that ladybird beetles played a smaller role in predating sentinel larvae compared with stinkbugs ($F_{3,28} = 7.78$, $P < 0.001$; Fig. 2.6a). Further, the combined effect of stinkbugs and ladybird beetles on larval predation (10%) was not significantly different from the effect of stinkbugs alone. However, there was a significant difference between observed and predicted larval predation in the combined natural enemy treatment ($F_{1,14} = 5.14$, $P = 0.040$), indicating an antagonistic interaction between stinkbugs and ladybird beetles. Total larval predation declined 64% in the presence of both predators relative to stinkbugs alone. Thus, larval predation by stinkbugs was constrained by antagonistic interactions with ladybird beetles.

In contrast to results with larval predation, egg predation was significantly higher in the presence of ladybird beetles than in treatments without them, while egg predation by stinkbugs was negligible ($F_{3,28} = 7.78$, $P < 0.001$; Fig 2.6b). However, unlike larval predation, the combination of predators neither strengthened nor weakened egg predation. The observed combined effect of stinkbugs and ladybird beetles on egg predation was not significantly different from those predicted based on the sum of each individual predator effect ($F_{1,14} = 0.07$, $P = 0.794$), suggesting that these predators had an additive effect on egg predation.

Discussion

We demonstrated that the local effectiveness of predator augmentation is moderated by the composition of the surrounding landscape. Indeed, predator releases had positive trophic cascading effects that increased predation rates, reduced pest abundance and plant damage, and increased crop biomass in complex landscapes. In contrast in simple landscapes, predator releases had a negative effect on pest control, increasing plant damage and reducing crop

biomass. Thus, the interaction between local augmentative biocontrol and landscape composition not only influenced the intermediate ecosystem service of pest control, but also had downstream consequences at the crop production level. Importantly, neglecting the landscape-mediated effects on the efficacy of predator augmentation may lead to inconsistent and misleading outcomes, which ultimately has consequences for growers who wish to implement this practice. While we recognize the potential implications of our findings for the management of lepidopteran pests in the cabbage system, our discussion here focuses on identifying the ecological mechanisms underlying the variation in the effectiveness of augmentative strategies. Knowledge of these mechanisms is key to increasing our ability to predict and understand when enemy augmentation can lead to net positive effects on pest control in a wide range of cropping systems.

Landscape effects on naturally occurring enemies. - Previous work has illustrated the importance of naturally occurring predators and parasitoids for lepidopteran pest suppression at the field scale (Schmaedick and Shelton 2000, Shelton et al. 2002). Here, we build on those studies by showing that the abundance of naturally occurring enemies are directly influenced by the composition of the landscape surrounding our focal fields. Simple landscapes, defined as landscapes with high proportions of cropland, were positively correlated with the abundance of foliar and ground-dwelling predators (based on the control plots). In contrast to predators, parasitoids were far less abundant in simple landscapes. These results indicate that the relative contribution of different naturally occurring enemies to pest suppression varies across the landscape complexity gradient, as reported elsewhere (Tamburini et al. 2016, Dainese et al. 2017). On one hand, parasitoids were positively host density-dependent (i.e., positive relationship between host and parasitoid abundance), but by themselves were not capable of lowering pest abundance and concomitant plant damage. Ground beetles, on the other hand, showed stronger positive impacts on larvae biocontrol with subsequent reductions in plant damage particularly in simple landscapes, but their densities did not respond numerically to changes in pest density. Naturally occurring coccinellids showed no clear contribution in

reducing densities of pest larvae or plant damage, but they were positively associated with egg predation.

Interaction between landscape composition and predator augmentation.- Although our findings suggest that naturally occurring enemies can contribute to the regulation of *P. rapae* populations, their control levels varied significantly over the course of the growing season and among landscapes. Therefore, complementary strategies are desirable to achieve stable and economic pest control. Results from our study suggest that augmentative releases of predators have the potential to supplement the strength of pest control provided by naturally occurring enemies under certain ecological contexts. Over the course of our study, predation on sentinel larvae was consistently higher at sites supplemented with predators when compared with predation in control plots. Yet, predator augmentation failed to provide consistent control of naturally occurring pest larvae across sites, which is presumably tied to differences in landscape composition. While previous studies have identified a number of ecological mechanisms that may limit the effectiveness of augmentative biological control in the field (e.g., climatic constraints, release timing and release rates, quality control) (Collier and Van Steenwyk 2004, Stiling and Cornelissen 2005, Crowder et al. 2007), this is the first study highlighting the importance of landscape context in mediating the effectiveness of enemy augmentation as a pest management strategy.

Several non-mutually exclusive mechanisms could explain the landscape-moderated effectiveness of predator augmentation on pest control reported here: (1) functional complementarity among augmented and resident enemies in complex landscapes, (2) antagonistic interactions (i.e., intraguild predation and predator interference) among enemy species in simple landscapes, and (3) via landscape-mediated changes in the composition of the local enemy assemblage, which in turn may determine the sign and strength of interactions with the augmented predators.

First, landscape complexity can enhance the complementarity among augmented and resident enemies, and thereby the strength of pest suppression (Dainese et al. 2017). Complex

landscapes containing large amounts of semi-natural habitats can provide natural enemies with alternative food sources and suitable microhabitats that together might favor the coexistence of species with overlapping feeding niches (Staudacher et al. 2018). Indeed, habitat heterogeneity has been positively linked to reductions in antagonistic interactions among natural enemies, thus increasing overall pest control (Finke and Denno 2002, 2006, Janssen et al. 2007). Our results support the idea that increasing enemy abundance may have net positive effects on pest control and plant performance, but only in complex landscapes where habitat heterogeneity may create favorable conditions for complementarity between augmented and resident enemies.

Second, our results also provide empirical support to the notion that landscape simplification potentially increase antagonistic interactions among natural enemies by reducing the diversity of habitats that provide key foraging and nesting resources enabling species coexistence. The role of antagonism among natural enemies in the outcome of biological control can be particularly important in situations when generalist predators are released. For example, *P. maculiventris*, although thought to be an effective biocontrol agent of lepidopteran pests (López et al. 1976, De Clercq and Degheele 1994, De Clercq et al. 1998), can also potentially feed on other natural enemies of *P. rapae*, including predatory coccinellids and hymenopteran parasitoids (Hough-Goldstein et al. 1996, Mallampalli et al. 2002, De Clercq et al. 2003, Herrick et al. 2008). However, the extent to which increasing the abundance of *P. maculiventris* may lead to decreases in other natural enemies under field conditions was not reported prior to this study. In our study, the abundance of naturally occurring coccinellids decreased significantly following the introduction of *P. maculiventris* in simple landscapes. It is conceivable that some of the reduction in coccinellid abundance was due to the increase in dispersal from the experimental plots supplemented with *P. maculiventris* rather than actual predation. In line with this finding, Moran and Hurd (1994) recorded increased emigration rates of naturally occurring spiders in response to increased density of mantid predators. Regardless of the causal mechanism, increasing the abundance of *P. maculiventris* through augmentative releases in simple landscapes can negatively affect other predators, thereby reducing overall pest control. Although *P.*

maculiventris also reduced parasitoid abundance in complex landscapes, this effect did not disrupt overall control of *P. rapae* because parasitoids only occurred when pest densities were already high.

Third, we showed that predators can disrupt one another via non-trophic interactions in a controlled laboratory experiment, which was designed to mimick a simple landscape. The effectiveness of *P. maculiventris* in feeding on *P. rapae* larvae was numerically reduced in the presence of *H. convergens*, as compared with *P. maculiventris* acting alone. Thus, our laboratory experiment results were consistent with our field findings of reduced biocontrol of *P. rapae* in simple landscapes. Factors leading to reduced effectiveness of *P. maculiventris* in simplified landscapes may have included changes in predator or prey foraging activity induced by the presence of other predators (i.e., *H. convergens*) (Schmitz 1998, Davenport and Chalcraft 2013). Recent studies have shown that such behavioral effects are ubiquitous in biocontrol systems and potentially affect pest suppression (Snyder and Wise 1999, Prasad and Snyder 2004, Schmidt et al. 2014, Hermann and Landis 2017, Schmitz 2017), as demonstrated herein. In complex landscapes, some of the mechanisms of reducing niche overlap (e.g., spatial separation or the availability of alternative preys) must be acting to maintain the effectiveness of *P. maculivestris* despite the potential interference with other natural enemies. These results underscore the importance of considering non-trophic interactions (e.g., predator interference) in concert with intraguild predation when interpreting the outcomes of multiple-predator effects.

Finally, the landscape context may influence the effectiveness of augmentative biocontrol via changes in the composition of the naturally occurring enemies. Unlike our finding that augmentation effectiveness was inversely related to habitat simplification, augmentation of natural enemies has been used successfully for decades in greenhouses (Messelink et al. 2014), even though enclosed environments are arguably simpler than open-field crops. This counterexample suggests that factors other than habitat complexity can, in some cases, determine whether positive effects of predator augmentation are realized within diverse enemy communities. Compared with open field crops, greenhouses virtually lack any naturally

occurring enemies that could potentially interfere with the released agent. In fact, species richness and composition are important determinants of the range and direction of interactions among natural enemies (Long and Finke 2014), especially in open field crops where enemy communities, even in simplified landscapes, are more complex and diverse than those of greenhouses⁷¹. Because there is considerable variation in the responses of different enemy taxa to changes in landscape composition, it follows that predator augmentation effects may vary in response to shifts in the identities of the species present in the local community. Naturally occurring enemies may potentially disrupt augmented predators either directly through mutual interference or intraguild predation, or indirectly via reduction in prey densities through pest consumption. Therefore, the effectiveness of enemy augmentation is not determined solely by the landscape context, but by how the local enemy assemblage interacts with the augmented enemies. Such context-dependency in the interaction among enemies hinders the formation of general rules to predict the net effects of predator augmentation across systems. Our study, nevertheless, provides new insights into the mechanisms whereby the combination of augmented and resident enemies may be expected to enhance pest control, and thereby offer a conceptual framework to make plausible predictions that are amenable to further testing in other systems.

Taken together, our work clearly demonstrates that the benefits of natural enemy augmentation are landscape-dependent. As such, our work adds to a growing set of evidence that biological pest control is not simply a function of enemy diversity and abundance, but also the landscape context in which enemies interact (Caballero-López et al. 2012, Martin et al. 2013). Fortunately, some general rules of these landscape dependency patterns have started to emerge to provide instructive management of certain landscape contexts where local agricultural practices may be more likely to enhance biological control. For example, planting flower strips adjacent to crop fields tends to produce large effects on boosting natural enemy populations in simple landscapes, but reduced impacts in complex landscapes (Jonsson et al. 2015). Other agri-environmental schemes aimed at pest control also have been shown to be more effective in simple than complex landscapes (Concepción et al. 2012, Tamburini et al. 2016). However, our

study found landscape dependency patterns that differ from those described above, indicating that more research on augmentation practices is needed before broader conclusions can be drawn. For example, it would be important to verify the consistency of our results over multiple cropping seasons. Also, studies in other cropping systems and geographic regions are important to test the generality of our findings.

Conclusions

Augmentative biocontrol has long been recognized as a promising pest control alternative to conventional pesticide use when used as part of a comprehensive integrative pest management approach. However, the effectiveness of augmentative biocontrol to manage agricultural pests in field situations has been questioned because they have mixed records of success. Our research expands on previous work exploring the ecological factors associated with such conflicting outcomes (van Lenteren 2000, Collier and Van Steenwyk 2004) by demonstrating that the effectiveness of augmentation depends strongly on the composition of the surrounding landscape. In the context of our study region, augmentative biocontrol was more effective in suppressing lepidopteran pests in complex than in simple landscapes. Clearly, these results are system-dependent and the specifics arising from other enemy-pest systems can create idiosyncrasies that demand case-by-case consideration. For example, a different conclusion might be reached by considering other natural enemies (e.g., augmentation of specialist parasitoids) or different target pests (e.g., aphids and flea beetles). From an applied perspective, this context dependency can be frustrating, but it must be acknowledged if we hope to effectively integrate natural enemy augmentation strategies in agricultural production systems. To this end, we need to move beyond the debate concerning the merits of using multiple vs. single species introductions of natural enemies with little regard for the spatial patterns in agricultural landscapes (Ehler 1990, Pedersen and Mills 2004, Paredes et al. 2015). Ultimately, a greater understanding of landscape-moderated interactions between pests and their natural enemies would provide much needed information for pest management practitioners with respect to how and where natural enemy augmentation can be implemented more effectively.

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REFERENCES

- A-1 Unique Insect Control. 2017. Unique Products. <http://a-1unique.com/unique-products/>.
- Andaloro, J. T., K. B. Rose, a M. Shelton, C. W. Hoy, and R. F. Becker. 1983. Cabbage growth stages. *N. Y. Food and Life Sci. Bull.* 101:1–4.
- Bale, J. S., J. C. van Lenteren, and F. Bigler. 2008. Biological control and sustainable food production. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 363:761–776.
- Batáry, P., A. Báldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 278:1894–1902.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software* 67.
- 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. Biological sciences / The Royal Society* 273:1715–1727.
- Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51:890–898.
- Blaauw, B. R., and R. Isaacs. 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. *Biological Control* 91:94–103.
- Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution* 28:230–238.
- Bousquet, Y. 2010. *Illustrated Identification Guide to Adults and Larvae of Northeastern North American Ground Beetles (Coleoptera: Carabidae)*. Pensoft Se. Pensoft Publishers, Sofia-Moscow.
- 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, USA.
- Caballero-López, B., R. Bommarco, J. M. Blanco-Moreno, F. X. Sans, J. Pujade-Villar, M. Rundlöf, and H. G. Smith. 2012. Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biological Control* 63:222–229.
- Chalfant, R. B., W. H. Denton, D. J. Schuster, and R. B. Workman. 1979. Management of Cabbage Caterpillars in Florida and Georgia by Using Visual Damage Thresholds. *Journal of Economic Entomology* 72:411–413.
- 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., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14:922–932.
- De Clercq, P., and D. Degheele. 1994. Laboratory measurement of predation by *Podisus maculiventris* and *P. sagitta* (Hemiptera: Pentatomidae) on beet armyworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology* 87:76–83.
- De Clercq, P., G. Keppens, A. G., and D. Degheele. 1988. Laboratory rearing of the predatory stinkbug *Podisus sagitta* (Fab.) (Heteroptera: Pentatomidae). *Med. Fac. Landbouww. Rijksuniv. Gent* 53:1213–1217.
- De Clercq, P., F. Merlevede, I. Mestdagh, J. Vandendurpel, K. Mohaghegh, and D. Degheele. 1998. Predation on the tomato looper *Chrysodeixis chalcites* (Esper) (Lep., Noctuidae) by *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas) (Het., Pentatomidae). *Journal of Applied Entomology* 122:93–98.
- De Clercq, P., I. Peeters, G. Vergauwe, and O. Thas. 2003. Interaction between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control

- in greenhouse crops. *BioControl* 48:39–55.
- Collier, T., and R. Van Steenwyk. 2004. A critical evaluation of augmentative biological control. *Biological Control* 31:245–256.
- Concepción, E. D., M. Díaz, and R. A. Baquero. 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landscape Ecology* 23:135–148.
- Concepción, E. D., M. Díaz, D. Kleijn, A. Báldi, P. Batáry, Y. Clough, D. Gabriel, F. Herzog, A. Holzschuh, E. Knop, E. J. P. Marshall, T. Tschardt, and J. Verhulst. 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology* 49:695–705.
- Costamagna, A. C., W. N. Venable, and N. A. Schellhorn. 2015. Landscape-scale pest suppression is mediated by timing of predator arrival. *Ecological Applications* 25:1114–1130.
- Cranshaw, W., D. C. Sclar, and D. Cooper. 1996. A review of 1994 pricing and marketing by suppliers of organisms for biological control of arthropods in the United States. *Biological Control* 6:291–296.
- Crowder, D. W., A. Nicolas, R. Al Mohamad, T. Hance, R. G. Adams, R. J. Prokopy, R. Albajes, D. W. Crowder, L. A. Gilkeson, T. Hance, F. Kohandani-Tafresh, F. Munaut, K. M. Harris, J. Havelka, R. Zemek, H. E. Hinton, L. A. Holmes, S. L. Vanlaerhoven, J. K. Tomberlin, Y. S. Jeoung, M. J. Seo, Y. N. Youn, Y. S. Choe, I. S. Oh, K. H. Han, B. R. Krasnov, I. S. Khokhlova, L. J. Fielden, N. V. Burdelova, V. Křivan, J. Havelka, E. M. Kroeker, V. K. Walker, É. Lucas, J. Brodeur, C. Luz, J. Fargues, M. Markkula, K. Tittanen, and V. B. Wigglesworth. 2007. Impact of release rates on the effectiveness of augmentative biological control agents. *Journal of insect science (Online)* 7:15.
- Dainese, M., G. Schneider, J. Krauss, and I. Steffan-Dewenter. 2017. Complementarity among natural enemies enhances pest suppression. *Scientific Reports* 7:1–8.
- Davenport, J. M., and D. R. Chalcraft. 2013. Nonconsumptive effects in a multiple predator system reduce the foraging efficiency of a keystone predator. *Ecology and Evolution*

3:3063–3072.

- Dray, S., and A. B. Dufour. 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software* 22:1–20.
- 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.
- Ehler, L. E. 1990. Introduction strategies in biological control of insects. Pages 111–134 *in* M. Mackauer, L. E. Ehler, and J. Roland, editors. *Critical Issues in Biological Control*. Intercept, Andover.
- Finke, D. L., and R. F. Denno. 2002. Intraguild Predation Diminished in Complex-Structured Vegetation : Implications for Prey Suppression. *Ecology* 83:643–652.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: The role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299–1306.
- Finke, D. L., and R. F. Denno. 2006. Spatial refuge from intraguild predation: Implications for prey suppression and trophic cascades. *Oecologia* 149:265–275.
- Frank van Veen, F. J., R. J. Morris, and H. C. J. Godfray. 2006. Apparent Competition, Quantitative Food Webs, and the Structure of Phytophagous Insect Communities. *Annual Review of Entomology* 51:187–208.
- Gabriel, D., S. M. Sait, J. A. Hodgson, U. Schmutz, W. E. Kunin, and T. G. Benton. 2010. Scale matters: The impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* 13:858–869.
- Gámez-Virués, S., D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. de Jong, N. K. Simons, A.-M. Klein, J. Krauss, G. Maier, C. Scherber, J. Steckel, C. Rothenwöhrer, I. Steffan-Dewenter, C. N. Weiner, W. Weisser, M. Werner, T. Tschardtke, and C. Westphal. 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications* 6:8568.
- 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, G. E. Heimpei, S. E. Applications, N. Jan, M. O. Neal, and C. D. Difonzo. 2009. Landscape Diversity Enhances Biological Control of an Introduced Crop Pest in the Published by : Ecological Society of America Linked references are available on JSTOR for this article : Your use of the JSTOR archive indicates your acceptance of the Terms. *Ecological Applications* 19:143–154.
- Garratt, M. P. D., D. Senapathi, D. J. Coston, S. R. Mortimer, and S. G. Potts. 2017. The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agriculture, Ecosystems and Environment* 247:363–370.
- Grab, H., B. Danforth, K. Poveda, and G. Loeb. 2018. Landscape simplification reduces classical biological control and crop yield. *Ecological Applications* 28:348–355.
- Herlihy, A. M. V, R. G. Van Driesche, M. R. Abney, J. Brodeur, R. A. Casagrande, D. A. Delaney, T. E. Elkner, S. J. Fleischer, D. S. Gruner, J. P. Harmon, G. E. Heimpel, K. Hemady, T. P. Kuhar, A. M. Shelton, A. J. Seaman, M. Skinner, R. Weinzierl, K. V Yeargan, and Z. Szendrei. 2012. Distribution of *Cotesia rubecula* (Hymenoptera : Braconidae) and Its Displacement of *Cotesia glomerata* in Eastern North America. *Florida Entomologist* 95:461–467.
- Hermann, S. L., and D. A. Landis. 2017. Scaling up our understanding of non-consumptive effects in insect systems. *Current Opinion in Insect Science* 20:54–60.
- Herrick, N. J., S. R. Reitz, J. E. Carpenter, and C. W. O'Brien. 2008. Predation by *Podisus maculiventris* (Hemiptera: Pentatomidae) on *Plutella xylostella* (Lepidoptera: Plutellidae) larvae parasitized by *Cotesia plutellae* (Hymenoptera: Braconidae) and its impact on cabbage. *Biological Control* 45:386–395.
- Homburg, K., N. Homburg, F. Schäfer, A. Schuldt, and T. Assmann. 2013. Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity* 7:195–205.
- Hough-Goldstein, J., J. Cox, and A. Armstrong. 1996. *Podisus maculiventris* (Hemiptera : Pentatomidae) Predation on Ladybird Beetles (Coleoptera : Coccinellidae). *The Florida*

Entomologist 79:64–68.

- Hughes, A. R., and J. H. Grabowski. 2006. Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia* 149:256–264.
- Janssen, A., M. W. Sabelis, S. Magalhães, M. Monserrat, and T. van der Hammen. 2007. Habitat Structure Affects Intraguild Predation. *Ecology* 88:2713–2719.
- Johnson, M. T. J., J. A. Bertrand, and M. M. Turcotte. 2016. Precision and accuracy in quantifying herbivory. *Ecological Entomology* 41:112–121.
- Jonsson, M., C. S. Straub, R. K. Didham, H. L. Buckley, B. S. Case, R. J. Hale, C. Gratton, and S. D. Wratten. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* 52:1274–1282.
- Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L. Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O’Rourke, A. Rusch, K. Poveda, M. Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tschardt, S. D. Wratten, W. Zhang, A. L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J. Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R. Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L. Cayuela, M. Centrella, A. Četković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M. H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D. Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr, Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseeth, D. J. Inclán, A. J. Ingrao, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N. Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa, D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F. Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P. Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M. E. O’Neal, I.

- Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D. Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M. Philpott, M. Plantegenest, M. Plečáň, T. Pluess, X. Pons, S. G. Potts, R. F. Pywell, D. W. Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J. Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K. Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J. Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W. van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A. Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115:E7863–E7870.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82.
- Landis, D. A., M. M. Gardiner, W. van der Werf, and S. M. Swinton. 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 105:20552–20557.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology* 45:175–201.
- van Lenteren, J. C. 2000. Measures of success in biological control of arthropods by augmentation of natural enemies. Pages 77–103 in G. Gurr and S. Wratten, editors. *Measures of success in biological control*. Springer Netherlands, Dordrecht.
- van Lenteren, J. C. 2012. The state of commercial augmentative biological control: Plenty of natural enemies, but a frustrating lack of uptake. *BioControl* 57:1–20.
- Lenth, R., Singmann H., Love J., Buerkner P., H. M. 2018. emmeans: Estimated Marginal Means, aka LeastSquares Means.
- Letourneau, D. K., I. Armbricht, M. C. Salguero-Rivera, B. Montoya-Lerma, J. Jiménez-Carmona, E. Daza, S. Escobar, V. Galindo, C. Gutiérrez, S. Duque-López, J. López-Mejía,

- A. M. Acosta-Rangel, J. Herrera-Rangel, L. Rivera, C. A. Saavedra, A. M. Torres, and A. Reyes-Trujillo. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications* 21:9–21.
- 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. Sivapragasam, 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, Shanhai, Taiwan. Asian Vegetable Research and Development Center.
- Long, E. Y., and D. L. Finke. 2014. Contribution of Predator Identity to the Suppression of Herbivores by a Diverse Predator Assemblage. *Environmental Entomology* 43:569–576.
- López, J. D., R. L. Ridgway, and R. E. Pinnell. 1976. Comparative Efficacy of Four Insect Predators of the Bollworm and Tobacco Budworm. *Environmental entomology* 5:1160–1164.
- Luke, S. G. 2017. Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods* 49:1494–1502.
- Lundgren, J. G., and G. E. Heimpel. 2002. Comparison of *Trichogramma brassicae* (Hymenoptera : Trichogrammatidae) Augmentation with Organic and Synthetic Pesticides for Control of Cruciferous Lepidoptera. *Environmental Entomology* 31:1231–1239.
- MacArthur, R. H. 1972. *Geographical ecology: Patterns in the distribution of species*. Harper & Row, New York.
- Mallampalli, N., I. Castellanos, and P. Barbosa. 2002. Evidence for intraguild predation by *Podisus maculiventris* on a ladybeetle, *Coleomegilla maculata*: Implications for biological control of Colorado potato beetle, *Leptinotarsa decemlineata*. *BioControl* 47:387–398.
- 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 of the United States of America* 110:5534–5539.
- Meehan, T. D., B. P. Werling, D. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the National Academy of Sciences of the United States of America* 108:11500–11505.
- Messelink, G. J., J. Bennison, O. Alomar, and B. L. Ingegno. 2014. Approaches to conserving natural enemy populations in greenhouse crops : current methods and future prospects. *BioControl* 59:377–393.
- Moran, M. D., and L. E. Hurd. 1994. Short-Term Responses to Elevated Predator Densities : Noncompetitive Intraguild Interactions and Behavior. *Oecologia* 98:269–273.
- Morandin, L. A., R. F. Long, and C. Kremen. 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. *Agriculture, Ecosystems and Environment* 189:164–170.
- Morandin, L. A., R. F. Long, and C. Kremen. 2016. Pest control and pollination cost-benefit analysis of hedgerow restoration in a simplified agricultural landscape. *Journal of Economic Entomology* 109:1020–1027.
- Östman, Ö., B. Ekbom, and J. Bengtsson. 2001. Landscape heterogeneity and farming practice influence biological control *Basic and Applied Ecology*. *Basic Appl. Ecol* 2:365–371.
- Paredes, D., L. Cayuela, G. M. Gurr, and M. Campos. 2015. Single best species or natural enemy assemblages? a correlational approach to investigating ecosystem function. *BioControl* 60:37–45.
- Pedersen, B. S., and N. J. Mills. 2004. Single vs. multiple introduction in biological control: The roles of parasitoid efficiency, antagonism and niche overlap. *Journal of Applied Ecology* 41:973–984.
- Philips, C. R., Z. Fu, T. P. Kuhar, A. M. Shelton, and R. J. Cordero. 2014. Natural History, Ecology, and Management of Diamondback Moth (Lepidoptera: Plutellidae), With Emphasis on the United States. *Journal of Integrated Pest Management* 5:1–11.

- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. R Development Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package version 3.1-122 R package:1–3.
- Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-Plus. Springer VerlagNewYork:528.
- Planet-Natural. 2018. Products.
- Poveda, K., E. Martínez, M. F. Kersch-Becker, M. A. Bonilla, and T. Tschardt. 2012. Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. *Journal of Applied Ecology* 49:513–522.
- Prasad, R. P., and W. E. Snyder. 2004. Predator interference limits fly egg biological control by a guild of ground-active beetles. *Biological Control* 31:428–437.
- Rincon-Vitova. 2018. Predator Bulletins.
- Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, and D. Kleijn. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters* 16:912–920.
- Scherr, S. J., and J. A. McNeely. 2008. Biodiversity conservation and agricultural sustainability: Towards a new paradigm of “ecoagriculture” landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:477–494.
- Schmaedick, M., S. A. M. 1999. Experimental Evaluation of Arthropod Predation on *Pieris rapae* (Lepidoptera : Pieridae) Eggs and Larvae in Cabbage. *Environmental Entomology* 28:439–444.
- Schmaedick, M. A., and A. M. Shelton. 2000. Arthropod predators in cabbage (Cruciferae) and their potential as naturally occurring biological control agents for *Pieris rapae* (Lepidoptera : Pieridae). *Canadian Entomologist* 132:655–675.
- Schmidt, J. M., T. O. Crist, K. Wrinn, and A. L. Rypstra. 2014. Predator interference alters foraging behavior of a generalist predatory arthropod. *Oecologia* 175:501–508.
- Schmitz, O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. *F1000Research* 6:1767.

- Schmitz, O. J. 1998. Direct and Indirect Effects of Predation and Predation Risk in Old-Field Interaction Webs. *The American Naturalist* 151:327–342.
- Shelton, A. M., W. T. Wilsey, E. R. Hoebeke, and M. A. Schmaedick. 2002. Parasitoids of cabbage Lepidoptera in central New York. *Journal of Entomological Science* 37:270–271.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Snyder, W. E., and D. H. Wise. 1999. Predator interference and the establishment of generalist predator populations for biocontrol. *Biological Control* 15:283–292.
- Staudacher, K., O. Rennstam Rubbmark, K. Birkhofer, G. Malsher, D. Sint, M. Jonsson, and M. Traugott. 2018. Habitat heterogeneity induces rapid changes in the feeding behaviour of generalist arthropod predators. *Functional Ecology* 32:809–819.
- Stiling, P., and T. Cornelissen. 2005. What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biological Control* 34:236–246.
- Straub, C. S., and W. E. Snyder. 2012. Increasing Enemy Biodiversity Strengthens Herbivore Suppression on Two Plant Species. *Ecology* 89:1605–1615.
- Szendrei, Z., A. Bryant, D. Rowley, M. J. Furlong, M. Schmidt, M. H. Greenstone, Z. Szendrei, A. Bryant, D. Rowley, and M. J. Furlong. 2014. Linking habitat complexity with predation of pests through molecular gut-content analyses. *Biocontrol Science and Technology* 24:1425–1438.
- Tamburini, G., S. De Simone, M. Sigura, F. Boscutti, and L. Marini. 2016. Conservation tillage mitigates the negative effect of landscape simplification on biological control. *Journal of Applied Ecology* 53:233–241.
- Team, R. 2015. R Development Core Team. *R: A Language and Environment for Statistical Computing* 55:275–286.
- Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43:294–309.

- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecology Letters* 8:857–874.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batary, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Frond, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87:661–685.
- Tuck, S. L., C. Winqvist, F. Mota, J. Ahnström, L. A. Turnbull, and J. Bengtsson. 2014. Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. *Journal of Applied Ecology* 51:746–755.
- USDA-NASS. 2016. USDA, National Agricultural Statistics Services. New York c. Washington, D.C.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. First edition. Springer-Verlag New York, New York..

Table 2.1. Statistical models for the effects of landscape composition and potential interactions with predator releases on lepidopteran larval abundance, plant damage, crop biomass, predation rates, and natural enemy abundance. Statistical models were used to estimate mean and 95% CI of effect sizes for overall effects of augmentative predator releases (Fig. 2.2) and the interactions with landscape composition (Figs. 2.3, 2.4, & 2.5). Dashed lines represent interaction terms not included in the final models because they were not significant ($P > 0.05$). Boldface text indicates significant relationships ($P < 0.05$).

Response variables and predictors	d.f.	F	P-value
Lepidoptera abundance			
Cropland (1000 m)	1, 11.887	4.885	0.047
Treatment (control and predator releases)	1, 40.407	5.200	0.028
Interaction (cropland x treatment)	1, 40.918	4.797	0.034
Plant damage			
Cropland (2000 m)	1, 11.335	7.656	0.018
Treatment (control and predator releases)	1, 43.651	19.520	< 0.001
Interaction (cropland x treatment)	1, 43.617	23.079	< 0.001
Crop biomass			
Cropland (2000 m)	1, 12.707	0.584	0.459
Treatment (control and predator releases)	1, 43.513	10.107	0.003
Interaction (cropland x treatment)	1, 43.049	10.976	0.002
Predation on sentinel larvae			
Semi-natural areas (2000 m)	1, 30.273	1.820	0.187
Treatment (control and predator releases)	1, 32.988	4.355	0.045
Interaction (semi-natural x treatment)	-----	-----	-----
Predation on sentinel eggs			
Semi-natural areas (2000 m)	1, 11.505	0.128	0.727
Treatment (control and predator releases)	1, 26.408	5.229	0.030
Interaction (semi-natural x treatment)	1, 25.844	4.618	0.041
Ground-dwelling predators			
Cropland (2000 m)	1, 11.301	6.753	0.024
Treatment (control and predator releases)	1, 31.629	0.001	0.973
Interaction (cropland x treatment)	-----	-----	-----
Parasitoids			
Semi-natural areas (1000 m)	1, 33.140	2.447	0.127
Treatment (control and predator releases)	1, 28.234	4.880	0.035
Interaction (semi-natural x treatment)	1, 27.759	6.105	0.020
Foliar-foraging predators			
Semi-natural areas (500 m)		z-value²	P-value²
Treatment (control and predator releases)		-0.791	0.429
Interaction (semi-natural x treatment)		-5.121	< 0.001
		4.815	< 0.001

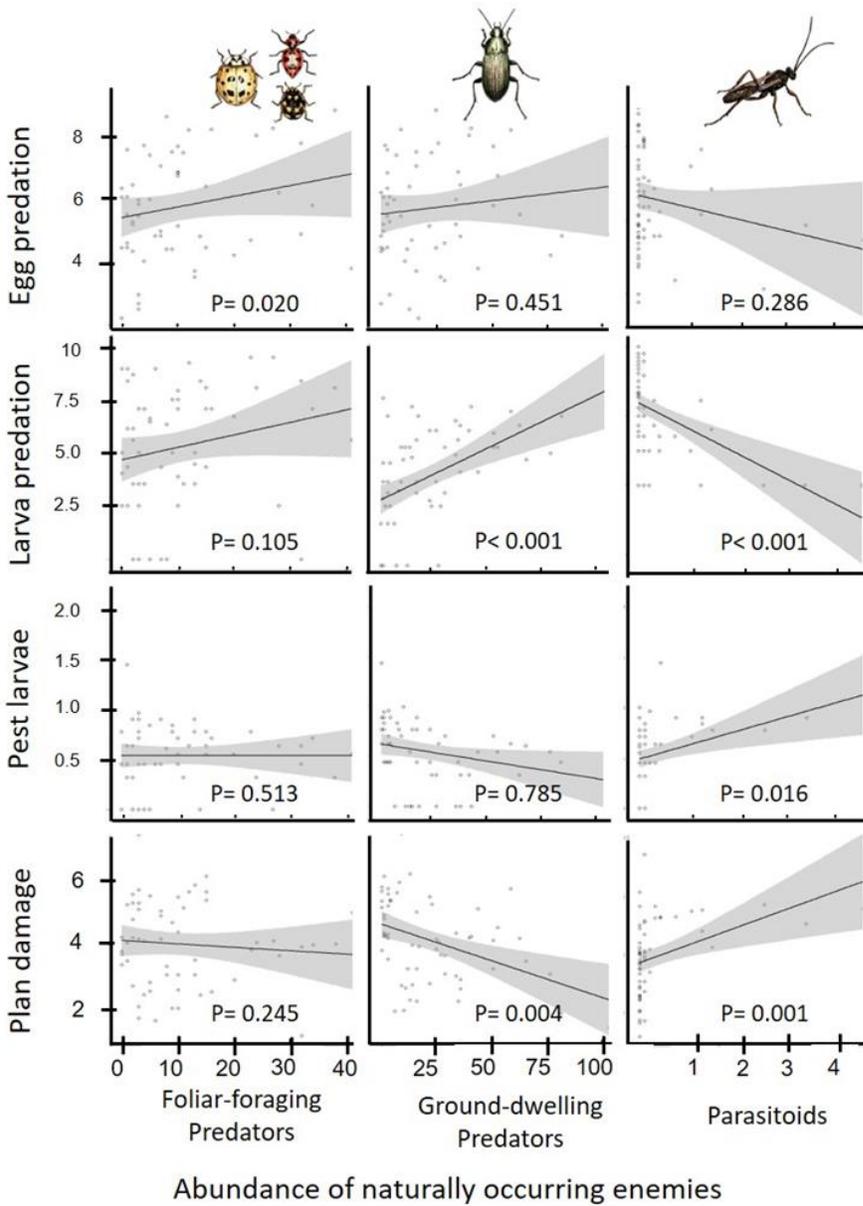


Fig. 2.1. Relationships between the abundance of naturally occurring enemies and predation on sentinel eggs, predation on sentinel larvae, natural incidence of lepidopteran larvae, and plant damage. All response variables were square-root transformed. Lines are the fixed-effect predictions and associated 95% confidence intervals (gray shaded).

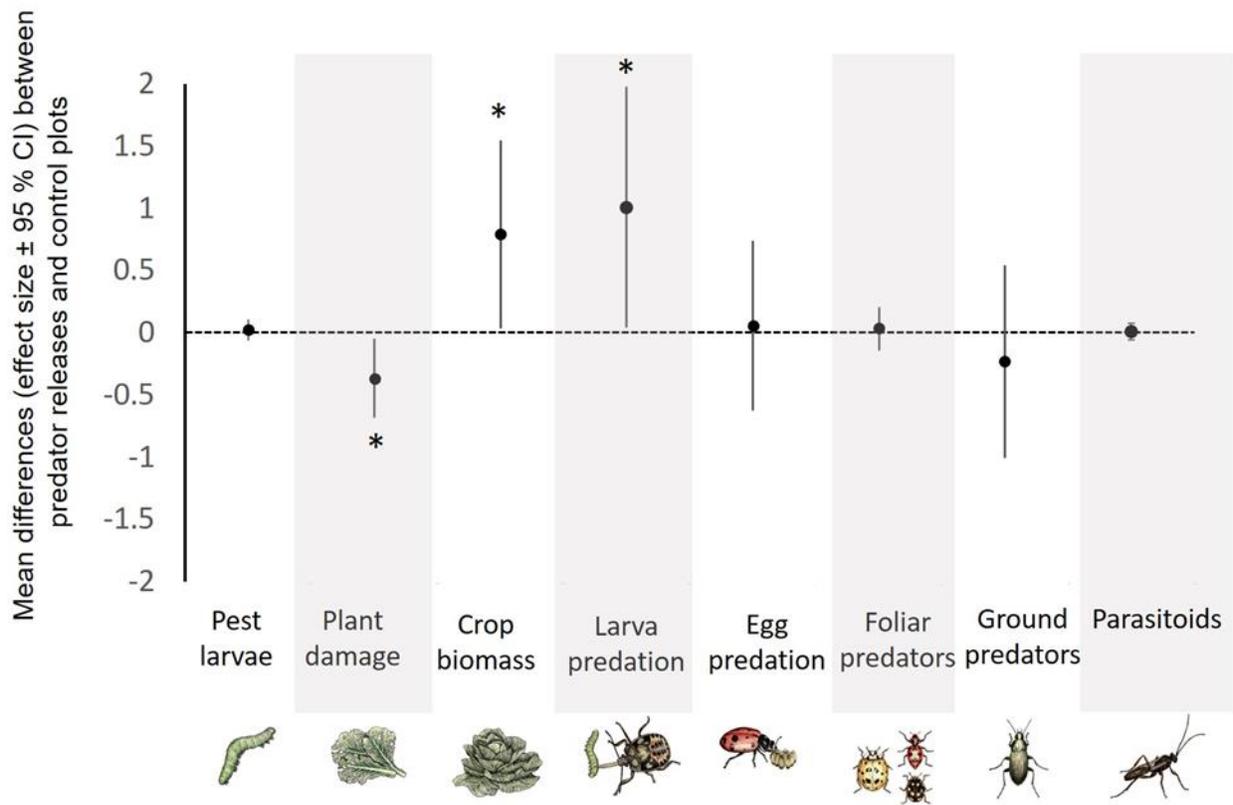


Fig. 2.2 Effect sizes (mean \pm 95% CI) for each response variable based on the difference in the marginal means between plots with and without augmentative predator releases. A positive effect size indicates that the mean of the predator release treatment is larger than the mean of control treatment, while a negative effect size indicates a higher control mean. Asterisks denote effect sizes that are significantly different from zero ($P < 0.05$). Summary statistics of the LMER and GLMM models used to estimate marginal means and confidence intervals are available in Table 1.

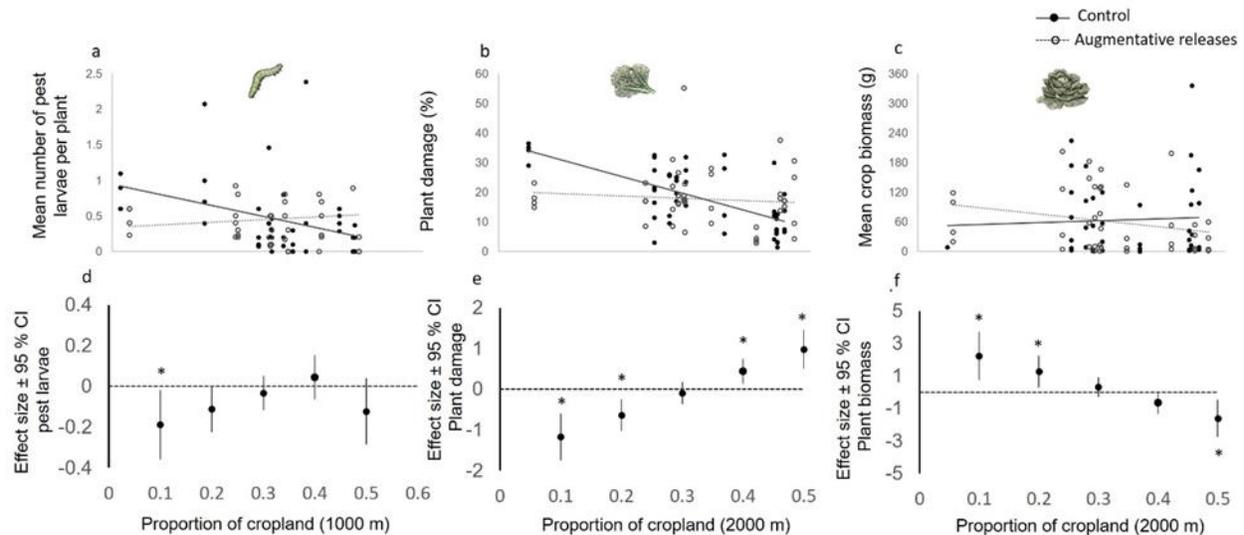


Fig. 2.3. The effect of augmentative releases of predators on (a) lepidopteran larval abundance, (b) plant damage, and (c) crop biomass in landscapes of varying complexity. Predicted responses for the control (solid lines) and augmentative releases (dashed lines) treatments are calculated from the set of best supported linear mixed-effects models (lme4). Effects of the interactions between treatment and landscape complexity were significant in all cases ($P < 0.05$). In the top Figures (a, b, and c) every point represents the mean treatment value in a given experimental plot for a given sampling period (i.e. 22 experimental plots and 4 sampling periods). The bottom figs. (d, e, and f) are effect sizes (mean \pm 95% CI) for lepidopteran larval abundance (d), plant damage (e) and crop biomass (f) based on the difference in the marginal means between plots with and without predator releases across the landscape complexity gradient. A positive effect size indicates that the mean of the predator plots is larger than the mean of control plots, while a negative effect size indicates a higher control mean. Pairwise comparisons were individually calculated at even intervals across the landscape complexity gradient. Asterisks denote effect sizes that are significantly different from zero ($P < 0.05$). Summary statistics of the LMER models used to estimate marginal means and confidence intervals are available in Table 1.

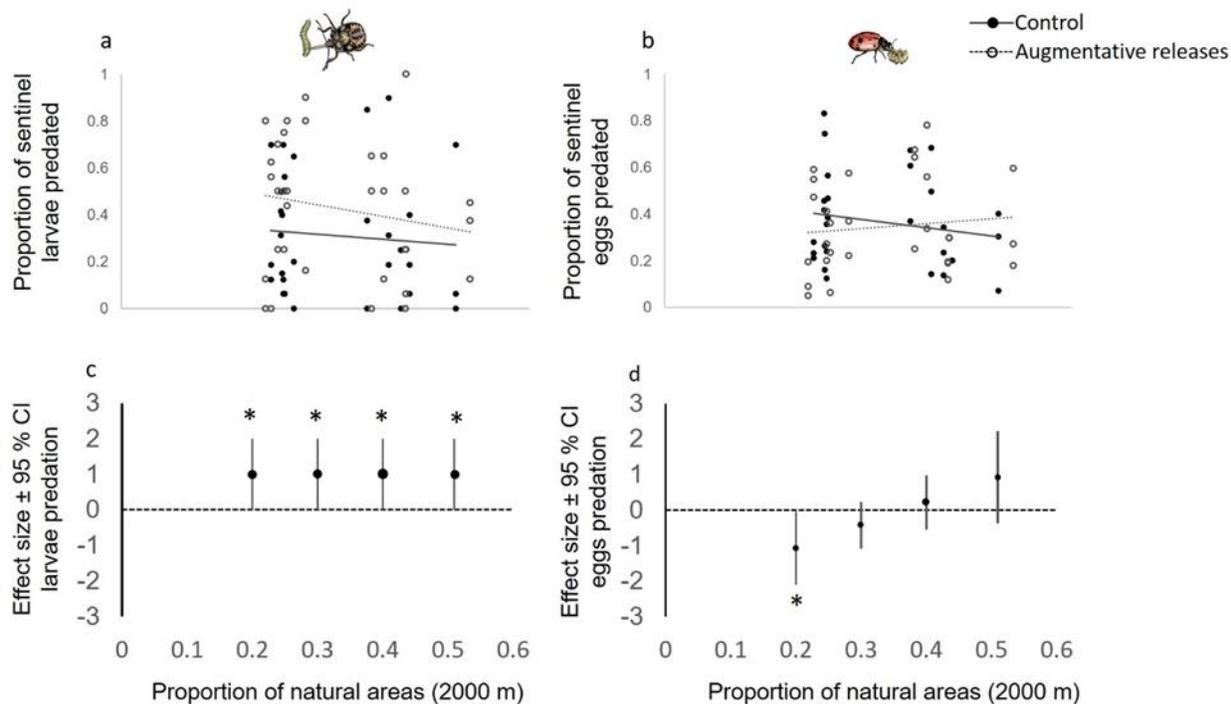


Fig. 2.4. The effect of augmentative releases of predators on (a) predation on sentinel larvae, and (b) predation on sentinel eggs in landscapes of varying complexity. Predicted responses for the control (solid lines) and augmentative releases (dashed lines) treatments are calculated from the set of best supported linear mixed-effects models (lme4). Effects of the interactions between treatment and landscape complexity were significant ($P < 0.05$) for egg predation, but not for larvae predation. In the top Figures (a and b) every point represents the mean treatment value in a given experimental plot for a given sampling period (i.e. 22 experimental plots and 3 sampling periods). The bottom figs. (c and d) are effect sizes (mean \pm 95% CI) for predation on sentinel larvae (c), and predation on sentinel eggs (c) based on the difference in the marginal means between plots with and without predator releases across the landscape complexity gradient. A positive effect size indicates greater predation rates in predator compared to control plots, while a negative effect size indicates lower predation rates in predator plots. Pairwise comparisons were individually calculated at even intervals across the landscape complexity gradient. Asterisks denote effect sizes that are significantly different from zero ($P < 0.05$). Summary statistics of the LMER models used to estimate marginal means and confidence intervals are available in Table 1.

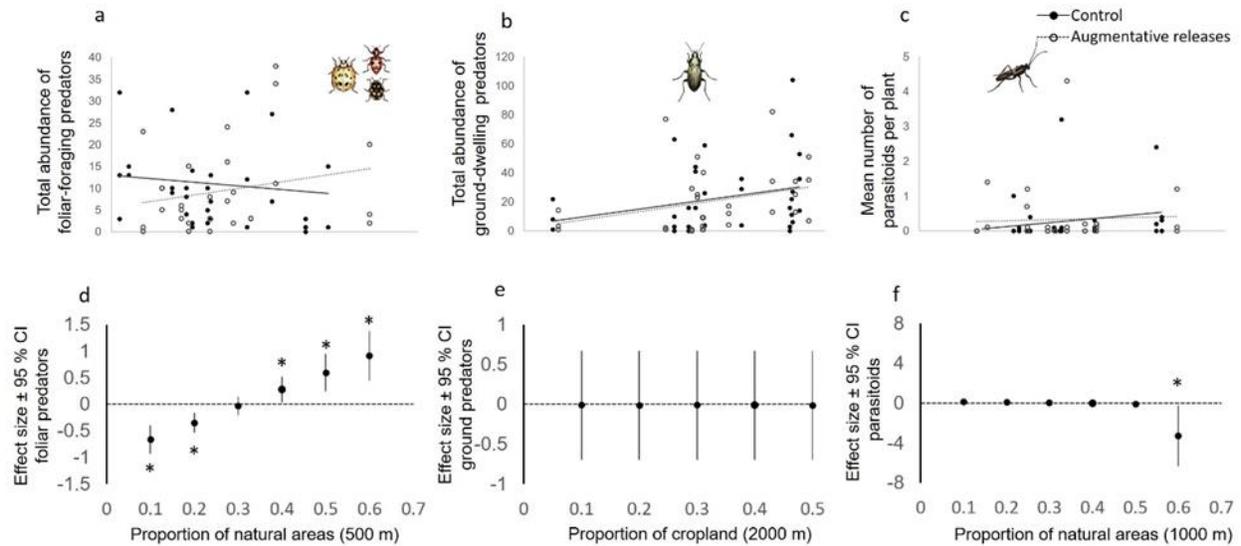


Fig. 2.5. The effect of augmentative releases of predators on (a) foliar-foraging predator abundance, (b) ground-dwelling predator abundance, and (c) parasitoid abundance in landscapes of varying complexity. Predicted responses for the control (solid lines) and augmentative releases (dashed lines) treatments are calculated from the set of best supported linear and generalized mixed-effects models (lme4). Effects of the interactions between treatment and landscape complexity were significant ($P < 0.05$) for foliar-foraging predators and parasitoid abundance. In the top Figures (a, b, and c) every point represents the mean treatment value in a given experimental plot for a given sampling period (i.e. 22 experimental plots and 3 sampling periods). The bottom figs. (d, e, and f) are effect sizes (mean \pm 95 % CI) for foliar predators (d), ground predators(e), and parasitoid abundance (f) based on the difference in the marginal means between plots with and without predator releases across the landscape complexity gradient. A positive effect size indicates higher abundance of natural enemies in predator compared to control plots, while a negative effect size indicates lower abundance of natural enemies in predator plots. Pairwise comparisons were individually calculated at even intervals across the landscape complexity gradient. Asterisks denote effect sizes that are significantly different from zero ($P < 0.05$). Summary statistics of the LMER and GLMER models used to estimate marginal means and confidence intervals are available in Table 1.

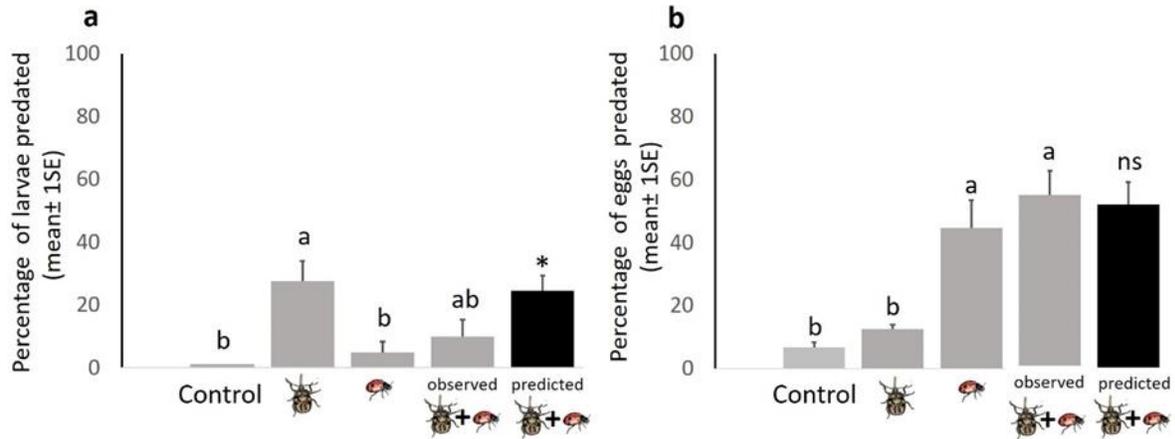


Fig. 2.6. Predation rates (mean \pm 1SE) on lepidopteran larvae (a) and eggs (b) under four treatments in the laboratory: (1) control, (2) stinkbugs alone, (3) ladybird beetles alone, and (4) stinkbugs with ladybird beetles. Different letters above bars indicate significant differences between treatments (two-way ANOVA followed by a Tukey HSD test, $p < 0.05$). Black bars represent predicted predation values for the combination of stinkbugs and ladybird beetles based on the multiplicative risk model (Sih et al. 1998). The asterisk indicates a significant difference in predation between observed and predicted values ($p < 0.05$). Back-transformed means \pm SE are presented but tests were performed using log-transformed data.

CHAPTER THREE

LANDSCAPE COMPOSITION MEDIATES THE RELATIONSHIP BETWEEN PREDATOR BODY SIZE AND PEST CONTROL

Abstract

Understanding the mechanisms contributing to positive relationships between predator diversity and natural pest suppression is fundamental to inform more effective management practices to support sustainable crop production. Predator body size can provide important insights to better understand and predict such predator-pest interactions. Yet, most studies exploring the link between predator body size and pest suppression have been conducted in species-poor communities under controlled environmental conditions, limiting our ability to generalize this relationship across heterogeneous landscapes. Using the community of ground beetles in cabbage fields, we examined how landscape composition (percent cropland) influences the size structure (mean, variance, and skewness of body size distribution) of predator communities and the subsequent effects on pest suppression. We found that predator communities shifted their size distribution towards larger body sizes in agriculturally dominated landscapes. This pattern arose from increasing numerical dominance of a few large-bodied species rather than an aggregated response across the community. Such landscape-driven changes in community size structure led to concomitant impacts on pest suppression, as the mean body size of predators was positively related to predation rates. Notably, the magnitude of pest suppression depended not only on the size of the dominant predators but was also strongly determined by the relative proportion of small vs. large-bodied species (i.e., skewness). Predation rates were higher in predator assemblages with even representation of small and large-bodied species relative to communities dominated by either large or small-bodied predators. Landscape composition may therefore modulate the relationship between predator body size and pest suppression by influencing the body size distribution of co-occurring species. Our study highlights the need to consider agricultural practices that not only boost effective predators, but also sustain a predator assemblage with a diverse set of traits to maximize overall pest suppression.

Key words: *Brassica oleracea*; biological control; ecosystem services; functional traits; ground beetles; landscape simplification; multi-predator effects; top-down control

Introduction

The growing concern over global declines in biodiversity has stimulated research into the consequences of species loss for ecosystem services (Cardinale et al. 2012). Although changes in the number of species is sometimes used as a proxy for explaining certain ecosystem functions and services (Cadotte et al. 2011), the link between predator species diversity and pest control is equivocal, with studies reporting negative, positive, and no relationships (Straub et al. 2008). Similarly, studies examining other facets of predator diversity, such as species evenness and phylogenetic diversity have also shown idiosyncratic responses in its relationships with pest suppression (Crowder et al. 2010, Griffin et al. 2013, Greenop et al. 2018). Understanding the mechanisms underpinning natural pest control could provide better insight into how biodiversity components could be manipulated for maximizing this pivotal ecosystem service.

In this context, extending the analysis beyond species diversity to focus on the functional traits directly linked to prey suppression provides an opportunity to elucidate the mechanisms that drive pest control services. Functional traits, such as body size, often determine the strength of species interactions (Rudolf 2012), and therefore how predator diversity affects pest suppression. Larger predators usually have higher per capita foraging rates than their small-bodied relatives (Ball et al. 2015), so increasing the average body size of predator communities can potentially induce stronger top-down control of pest densities (Russell et al. 2017). Research on predatory species also reveals that large individuals are able to reduce functional overlap with heterospecifics due to their ability to access and exploit a broader diversity of food resources (Cohen et al. 1993). Body size is a crucial determinant of niche overlap and intraguild predation within food webs (Woodward and Hildrew 2002), and therefore may increase our ability to predict the circumstances under which predator diversity can lead to positive biocontrol effects. Body size is also tightly linked to other life history traits, such as dispersal ability (Jenkins et al.

2007) and reproductive output (Peters 1983, Honěk 1993), which determines in part, species responses to environmental changes. Understanding variation in body size thus informs not only about ecosystem functioning, but also how species assemblages may change as a result of environmental perturbations.

Relationships between predator body size and pest suppression are, however, not consistent across systems. Inherent in most of the current trait-based approaches is the assumption that the functional role of species is relatively constant in different ecological contexts and unaffected by the presence of other species in the community assemblage. Yet, there is clear evidence that the functional role of species is not necessarily the same when species are in a mixture, relative to when species are in isolation (Griffin et al. 2013). This is because the presence of interspecific interactions occurring between diverse predator assemblages can positively or negatively affect the trait expression of individual species, altering aggregated contributions to pest control (Sih et al. 1998). While laboratory experiments suggest, for example, that per capita predation rates are positively associated with predator body size (Rouabah 2014), field studies report that communities dominated by large-bodied predators increase the opportunity for intraguild predation on small predators (Rusch et al. 2015), leading to a net decline in pest control. Likewise, small predators might alter the foraging behavior and habitat use of large predators (Prasad and Snyder 2004, Rudolf 2006, Davenport and Chalcraft 2013), in turn influencing pest suppression. Both the composition of predator body sizes and trophic interactions are likely important in determining the strength of pest suppression, however, the interplay between them is not well understood.

Another factor that may impact the relationships between predator body size and pest suppression is landscape context. Landscape context is important because increases in agricultural production have greatly altered land-use patterns, resulting in landscapes that are structurally simplified and dominated by croplands (Tscharntke et al. 2005). Landscape simplification may alter the distribution of predator body sizes not only through changes in species dominance (i.e., when large or small-bodied species become numerically dominant and

therefore exert a strong influence on the community mean body size), but also through changes in the functional community composition (i.e., the frequency distribution of different body size classes, herein body size diversity). This may occur because landscape simplification selects for or against species with a distinct set of traits (Gámez-Virués et al. 2015). For example, in Europe, small-bodied ground beetles are more abundant in crop-dominated landscapes than structurally complex landscapes (Kotze and O'Hara 2003). Such changes in body size distributions (i.e., relative proportion of small vs. large species) could have considerable consequences for pest control, particularly as ecosystem services are thought to be largely determined by the functional traits of dominant species (Balvanera et al. 2005, Tolkinen et al. 2013, Winfree et al. 2015). Furthermore, landscape simplification might lead to changes in predator body size diversity that, in turn, are expected to influence the strength of pest suppression. The intuitive interpretation that increasing predator size diversity might lead to niche complementarity and better biological control is not always generalizable, as increasing the size range of predators is also likely to increase the strength of indirect interactions among predators that can alter pest suppression in a landscape-dependent manner (Martin et al. 2013). Thus, land-use changes may modify relationships between predator body size and pest control through multiple pathways, which may not be predicted solely by changes in average body size. Previous research has documented how multiple aspects of body size structure (i.e., mean, diversity, and relative proportion of individuals across size classes) can influence pest suppression, but often these studies have been performed under controlled, simplified environments (e.g., Rudolf 2012, Rouabah et al. 2014, Jonsson et al. 2018). However, information is lacking on how these results scale up into realistic, more species rich-communities observed on farms across heterogeneous landscapes. In addition, few studies have explored the relative importance of concurrent changes on the mean, diversity, and shape of predator body size distributions on the strength of pest suppression.

We address these knowledge gaps by examining how landscape simplification affects body size structure of predator communities, and how these changes consequently influence pest

control. We used the community of ground beetles (Coleoptera: Carabidae) inhabiting cabbage fields as a model system. Ground beetles are sensitive to land-use changes, are taxonomically and functionally diverse, and are considered one of the most important group of predators of agricultural pests (Lövei and Sunderland 1996, Kromp 1999). Moreover, ground beetle communities differ widely in abundance and body size (2-40 mm) within their constituent species, which makes this group ideal for examining factors affecting body size distribution and subsequent impacts on pest suppression. Specifically, we asked (i) whether landscape simplification leads to shifts in the mean, diversity, and distribution of predator body sizes, (ii) whether body size structure matters for pest suppression and assessed the relative contribution of individual species in this relationship, and (iii) whether landscape context modulates the strength of the relationship between predator body size and pest suppression.

Methods

Study site

The study was conducted on 11 farms across a gradient of landscape simplification in the Finger Lakes Region of New York State (USA), during the summers of 2014 and 2015. On each farm, we established two 10 x10 m plots consisting of ten rows of cabbage (*Brassica oleracea* var. capitata cv. Capture) with 15 cabbage plants per row. All 44 experimental plots were planted on farms characterized as organic or that used minimal inputs for pest management. Plots received no insecticide or fungicide applications, and weeds were removed manually at two-week intervals. All plots were planted across study areas over two consecutive weeks in mid-June in both years.

Proportions of cropland and semi-natural areas around each plot were calculated using the National Agricultural Statistics Service Cropland Data Layer for New York (USDA-NASS 2016) in ARCGIS 10.3. Cropland in this region was comprised primarily of corn, soybean, winter wheat, and brassicas; while semi-natural habitats included shrubland, deciduous forest, woody wetlands, evergreen forest, and mixed forest. We quantified the cover of cropland and semi-natural habitats at three spatial extents: 500, 1000, and 2000 m. By fitting separate linear

mixed-effect models (lme) for each response variable and scale, we determined the proportion of cropland at 1000 m was the scale at which landscape composition provided the best fit to the data (based on the AICc values, see Appendix S3: Table S3.1). Earlier studies showed that the 1000 m spatial scale was relevant to understand the dynamics of ground beetle communities (Rusch et al. 2014, Winqvist et al. 2014, Hanson et al. 2016, Rush et al. 2016).

Ground beetle sampling, community structure, and body size measurement

The activity-density of adult ground beetles in the field was determined using pitfall traps. Each pitfall trap consisted of a 540 ml plastic cup (9 cm diameter openings, Fabri-kal corp., Kalamazoo, MI, USA) filled about one-third with a mixture of odorless detergent (Dr. Bronner's Unscented Pure Castile Soap, Vista, CA, USA) and water. The cups were inserted into the soil, with the rim at the soil surface, and protected from direct sunlight and rain with a plastic plate (25 cm diameter) positioned 10 cm above the trap. The traps were placed in the corners and center of each plot, for a total of five traps per plot. All pitfall traps were kept open for 24 h at four different times each year during seedling, pre-cupping, early head formation, and maturation growth stages (Andaloro et al. 1983). Carabid beetles were identified to species using both Lindroth (1961, 1963a, 1963b, 1966, 1968) and Bousquet (2010) taxonomic keys, following the classification of Bousquet and Laroche (1993). Following taxonomic identification, we gathered information from the literature to further classify carabids into three diet categories according to their predominant feeding habits during the adult stage: carnivorous, omnivorous or herbivorous (Bousquet 2010, Homburg et al. 2013) (Appendix S3: Table S3.3).

Plot-specific estimates of species richness (Shannon-Wiener), species evenness (Pielou's evenness), and activity-density of all carabid communities were calculated from pooled pitfall catches of each plot and sampling year. In addition, the sex of all specimens collected from each plot and sampling year was determined, and 15 males and 15 females were selected at random to measure body size. If there were fewer than 15 males or females per plot, then all available specimens were measured. Elytra length (i.e., the longest distance from the elytron apex to the elytron base) was digitally measured for all selected specimens using an Olympus SZX10

stereomicroscope connected to a computer installed with the micro imaging software cellSens (Olympus Corp., Tokyo, Japan). Elytra length is considered a good indicator of body size in ground beetle communities and has been used in previous studies (Juliano 1986, Nelemans 1987).

For each plot and sampling year, we calculated three complementary metrics to characterize community body size structure: community weighted mean (CWM), community weighted variance (CWV), and skewness (i.e., frequency distribution of body size classes). Community weighted mean is the mean body size value of the species present per plot weighted by their abundance, and reflects the trait values of dominant species in the community. Community weighted variance is the plot-level variance in body size values weighted by species abundance and represents a measure of size diversity. Community weighted variance was calculated following Gaüzère et al. (2019), with higher values occurring when communities have greater size diversity. Lastly, skewness was calculated by allocating species into different size categories on the basis of its log-transformed body size (mm). Following the Freedman-Diaconis rule to choose the appropriate number of classes (Birgé and Rozenholc 2006), we grouped individuals into six size categories that spanned the total range of body size in our study (1.5–13.7 mm). Then, we produced a histogram of the number of individuals in each size category and calculated the coefficient of skewness for each plot. Positive skew coefficients indicated right-skewed distributions (i.e., greater number of small-bodied individuals), values approaching zero indicated symmetric distributions (i.e., similar number of small and large-bodied species), and negative values denoted left-skewed distributions (i.e., greater number of large-bodied individuals). Skew body size distributions can inform whether trait filtering is occurring along the landscape gradient (i.e., shifts in community body size distribution). Metrics were calculated using the FD (Laliberté et al. 2015) and S3cR (Gaüzère et al. 2019) packages in R.

Predation rates in the field

Concurrently with carabid sampling, we conducted a sentinel prey experiment to determine the relationship between ground beetle community structure and predation rates. Predation rates were quantified using pupae of the economically important pest the diamondback moth (*Plutella xylostela*) obtained from a colony collected from cabbage fields, and maintained on a wheat germ-casein artificial diet (Shelton et al. 1991).

In each plot, ten circular plastic plates (9 cm diameter) were placed on the ground at least 1.5 m apart from each other in a 5x2 formation in the center of the plot. The plates were positioned so that the surface of each plate was level with the ground. A group of ten pupae was then placed in the center of each plate and left in the field for 24 h. At the end of this period, the number of removed pupae was recorded. We repeated this experiment three times per plot each year at 15, 30, and 45 days after transplanting, which covered crop development from seedling to early head formation stage.

Because other arthropods and small vertebrates might also be involved in pupal predation, we monitored one of the sentinel prey arenas per plot with a video camera to determine the relative contribution of ground beetles to overall predation rates (see Appendix S3: Supplementary Methods S3.1 for more details on the video surveillance of predation events). Video data revealed that ants (37%), carabid beetles (22%), and opiliones (18%) accounted for the majority of visits to sentinel prey, while prey visits by other predatory taxa collectively accounted for only 23% of the total visits (Appendix S3: Fig S3.1). Predation rates attributable to carabid beetles (P_{cb}) for each sentinel prey arena were calculated as:

$$P_{cb} = P_T \times V_{cb} / 10$$

where P_T is the total number of removed pupae on a given sentinel prey arena, V_{cb} is the proportion of total prey visits made by carabid beetles calculated from video observations of the given plot (see Appendix S3: Supplementary Methods S3.1), and 10 is the initial number of pupae per sentinel prey arena. We believe that our P_{cb} calculations represent a conservative estimate of the biocontrol potential exerted by carabid beetles. *Plutella xylostella* is not the only

pest in these landscapes (e.g., aphids, flea beetles, and cabbage root flies), and crops other than cabbage have additional pests that may be attacked by carabid beetles (Clark et al. 1997, Suenaga and Hamamura 2001). Indeed, carabid beetles are polyphagous predators that have the potential to maintain a wide range of pest species below outbreak levels (Kromp 1999, Menalled et al. 1999). Therefore, it is safer to interpret our predation rate estimates as comparative measures of biocontrol potential rather than absolute magnitudes of pest regulation by carabid beetles. Most importantly, our video analysis revealed no significant differences in the relative proportion of predation visits by carabid beetles along the landscape gradient (Appendix S3: Fig. S3.3), indicating that any potential bias in the accuracy of the method to estimate predation by carabid beetles is the same in all communities and thereby does not invalidate relationships found in our study.

Statistical analysis

Landscape effects on the mean, variation, and body size distribution. To determine whether species with a particular body size are specialized in some portions of the landscape gradient, we carried out a multivariate technique of constrained ordination, the Outlying Mean Index (OMI, Doledec et al. 2000). OMI used a plot-by-species abundance matrix as the response and the proportion of cropland at 1000 m radius as the predictor. This provided information regarding the niche position (i.e., mean conditions of occurrence) of each carabid species along the landscape gradient. Species with positive values along the OMI axis tended to occur in simple landscapes, and those with negative values tended to occur in complex landscapes. OMI also provided a measure of niche breadth (variance around the niche position). Species with high niche breadth values occur across a broad range of landscape conditions, whereas species with low niche breadth occur in a limited range of conditions. To test whether the mean body size of each species was significantly associated with its niche position (i.e., niche position on OMI axis) and niche breadth, we performed linear regression analyses. Calculations were performed using the package *ade4* (Dray and Dufour 2007).

To evaluate the effect of landscape simplification on the mean (CWM), diversity (CWV) and symmetry (skewness) of community body size distributions, we used linear mixed-effect models (nlme) with proportion of cropland in a 1000-m radius as a predictor variable. “Farm identity” and “year” were included as random effects in all models to account for any environmental differences across sites and years. Model assumptions were checked according to the graphical validation procedures recommended by Zuur et al. (2009). Significance of the models was assessed by conditional F-tests (Pinheiro and Bates 2000). No spatial autocorrelation was found in residuals of these models (Appendix S3: Table S3.2.).

Species-specific contributions to community body size change across the landscape gradient. To quantify the contribution of individual carabid species to community weighted mean (CWM), we followed the method proposed by Gaüzère et al. (2019). This method is based on a Jackknife procedure, where species are removed one by one from the data set and then the CWM is iteratively recalculated. The contribution of each species is estimated as the difference between CWM of the whole dataset and CWM values without a given species. Species with positive values contribute toward the CWM global trend, while negative values indicate species contributing against the overall trend. Furthermore, major contributors to the CWM trend are species with large fluctuation in relative abundance and extreme body sizes (e.g., an exceptionally large or small species) (Gaüzère et al. 2019).

To characterize the relative contribution of small and large species to community mean body size, we divided species into two discrete size categories based on a cluster analysis: small (1.5 - 6.2 mm), and large (7.3 - 13.7 mm) (see Appendix S3: Supplementary Methods S3.2 for details on the cluster analysis). Similarly, we categorized species according to functional group (i.e., carnivorous, herbivorous, and omnivorous) and estimated the collective contribution of each group to overall CWM trends across the landscape gradient.

Effects of ground beetle community structure on predation rates. Relationships between ground beetle community structure and predation on sentinel prey were examined using mixed effect models (nlme) with Gaussian error distributions. Response variable was defined as the

mean proportion of sentinel prey removed by carabid beetles across the season for a given plot and a given year. We fit separate models for each component of community structure (i.e., species richness, activity-density, species diversity, evenness, CMW, CWV, and size skewness). The initial fixed-effects included a community descriptor, proportion of cropland in the landscape in a 1000 m radius, and their interaction. “Farm identity” and “year” were included as random effects in all models. We then simplified the fixed-effects structure using backwards stepwise model simplification, where non-significant predictors were removed ($P > 0.05$). Statistical significance of fixed effects and their interactions were assessed by conditional F-tests (Pinheiro and Bates 2000). To evaluate which aspects of community structure better predicted predation rates, we selected models with the highest explanatory power by comparing the AIC values of the minimum adequate models (Burnham and Anderson 2002).

Lastly, we took advantage of the natural differences in body size distributions across the landscape to examine how changes in the relative proportion of small vs. large species influenced the relationship between body size and predation rates. Local carabid communities were grouped into three discrete classes on the basis of the shape of the body size distribution: (i) right-skewness (i.e., communities dominated by small-bodied species), (ii) left-skewness (i.e., communities dominated by large-bodied species), and (iii) symmetrical distribution (similar number of small and large-bodied species). To determine if the local body size distributions were significantly skewed, they were tested against normality using Shapiro-Wilks tests. Sample sizes for each group were as follows: right-skewness ($n = 19$), left-skewness ($n = 11$), and symmetrical distribution ($n = 12$). For each group, we then calculated the slopes of the relationships between CWM of body size and predation rates using simple linear regression analysis. We also evaluated whether predation rates between the three size distribution groups were significantly different using a one-way ANOVA followed by a Tukey’s multiple comparison test at $P < 0.05$. All analyses were conducted using R version 3.5.3.

Results

A total of 3378 carabids belonging to 47 species and 22 genera were collected in cabbage fields (Appendix S3: Table S3.3). Of these, 29 were small-bodied species (elytra length < 7.3 mm) which made up 58% of individuals collected, while the remaining 18 species were categorized as large (elytra length \geq 7.3 mm) representing 42% of the total capture (Appendix S3: Fig. S3.4).

The OMI analysis revealed different occupancy requirements and patterns of specialization between large and small-bodied beetles (Fig. 3.1). Large-bodied beetles tended to occur in more simple landscapes (i.e., positive niche values) and exhibited a narrower niche breadth than small-bodied beetles (Fig. 3.1b-c). On average, niche breadth for small beetles was 2.4 times higher than for large beetles, indicating that small beetles are distributed along a wider variety of landscape conditions (Fig. 3.1c). These overall patterns were followed for some, but not all, species. In fact, species within the same size class displayed great variation in both niche position and niche breadth (Fig. 3.1a).

At the community level, landscape simplification had a clear effect on the functional composition of the dominant species (Fig. 3.2a). Landscape simplification promoted a shift to communities dominated by large-bodied species (i.e., negative skewness), while complex landscapes were numerically dominated by small-bodied species (i.e., positive skewness) ($F_{1,20} = 9.088$, $P = 0.007$). Importantly, we detected no change in body size diversity (i.e., community-weighted variance) across the landscape gradient ($F_{1,19} = 0.726$, $P = 0.405$; Fig. 3.2b), indicating that the observed shifts in body size distributions arose from changes in the relative proportion of small vs. large species, rather than a net change in the number of species. Indeed, we found no significant differences in species richness, i.e., the number of species, across the landscape gradient ($F_{1,19} = 3.796$, $P = 0.066$; Appendix S3: Fig. S3.5).

The community-weighted mean (CWM) for predator body size increased with the proportion of cropland in the surrounding landscape ($F_{1,20} = 4.775$, $P = 0.041$; Fig. 3.2c). Overall, predator body size increased by about 35% from complex to simple landscapes. When

considering the contributions of each species separately, we found that only 16 of the 47 species collected shaped CWM trends, whereas the remaining species exhibited negligible contributions (Fig. 3.3a). These results indicated that the overall trend towards increasing mean body size as landscapes became simpler was largely driven by changes in the relative proportion of a few dominant species, rather than a community-wide shared response. Species driving this overall trend were large-bodied species whose abundances increased in simple landscapes (e.g., *Poecilus chalcites* and *Pterostichus melanarius*) and small-bodied species with decreased abundance across the landscape simplification gradient (e.g., *Elaphropus anceps*, and *Bembidion quadrimaculatum*) (Fig. 3.3a-b). Specifically, *Poecilus chalcites* and *Elaphorus anceps* were the top two species that together accounted for 50% of the community mean increase in body size in simple landscapes (Fig. 3.3a). Other species tended to decrease CWM along the landscape simplification gradient (i.e., large-bodied species with decreased abundance in simple landscapes or small-bodied species with increased abundance in simple landscapes), and therefore had a negative contribution to overall trends. As with positive contributors, only a few species were substantially contributing against the global CWM trends (i.e., *Harpalus puncticeps* and *Harpalus rufipes*). Carabid functional groups also made different contributions to CWM trends, with carnivorous and omnivorous species having net positive contributions, while phytophagous species were largely responsible for negative contributions (Fig. 3.3c).

Predation on sentinel prey was not predicted by any of the taxonomic-based indices (i.e., species richness, evenness, species diversity), activity-density, size diversity (CWW) or by size distribution (skewness) of ground beetle communities (Appendix S3: Fig. S3.6 and Table S3.4). In contrast, we found a positive relationship between community weighted mean body size (CWM) and the number of sentinel pupae predated in the field ($F_{1,19} = 9.194$, $P = 0.006$; Fig. 3.4a). Predation rates were, on average, two-fold greater in plots with higher CWM predator body size (i.e., > 6 cm) relative to plots with lower CWM (i.e., < 4 cm). While we detected an overall positive relationship between increasing body size and predation rates, this pattern was not consistent across communities (Fig. 3.4b). Communities dominated by large-bodied species

or with similar number of small and large individuals, showed a significant positive relationship between increasing predator body size and predation rates. In contrast, there was no significant relationship in communities dominated by small-bodied species. Furthermore, there was a 2.3-fold variation among communities in the magnitude of the effect on how changes in predator body size affected predation rates ($F_{2,39} = 22.73$, $P < 0.001$; Fig. 3.4c). Interestingly, predation rates peaked in places that harbored communities with even representation of small and large species. These results indicated that the consequences of increasing predator body size on the strength of top-down control depended upon the body size distributions of co-occurring species that, in turn, were influenced by landscape context.

Discussion

We found that landscape simplification, associated with increasing cropland, influenced the body size distribution of predator communities. Overall, predator communities shifted their size distribution towards larger body sizes with increasing landscape simplification. This pattern arises from increasing numerical dominance of a few large-bodied species rather than an aggregated response across multiple species in the community. Indeed, only 3 species (6% of the total 47 species collected) were responsible for 54% of the community body size changes across the landscape gradient (i.e., *P. chalcites*, *P. lucublandus*, and *P. melanarius*). Such landscape-driven changes in community body size structure may lead to concomitant impacts on ecosystem functioning, as the average body size was positively related to predation rates on sentinel prey. Thus, our results highlight body size as a key predictor of pest suppression, as it affects both the way species respond to land-use changes and mediate the strength of trophic interactions.

Landscape simplification had clear effects on predator body size. We found that plots in complex landscapes favored a greater abundance of small-bodied species, while plots from simple landscapes were numerically dominated by large-bodied species. Contrary to our findings, previous studies have shown that increased landscape simplification lead to lower average body size of multiple invertebrate taxa (Tsiafouli et al. 2015). Instead, our results are in line with results of recent studies showing that ground beetle communities can benefit from

landscape simplification (Winqvist et al. 2011, Rusch et al. 2016). In fact, several of the large-bodied species collected in this study are relatively well adapted to habitats with open and sparse vegetation such as croplands (e.g., *Pterostichus* spp. and *Poecilus* spp., Bousquet 2010), where they can overwinter and take advantage of the high prey availability (Rand and Tscharrntke 2007). Importantly, this variation in body size distribution of predator communities occurred without any detectable change in predator richness along the landscape gradient. This suggests that landscape variation in body size distributions may serve as an early indicator for detecting potential changes in pest control provision that occur before, or even in the absence of, declines in species richness.

Quantifying the contribution of individual predator species to overall prey suppression within a multispecies assemblage would be a formidable undertaking. Rather, current practice is to assess the ecological role of species indirectly via their functional traits (Díaz et al. 2013, Perović et al. 2017). Here, we demonstrated that body size is indeed an important determinant of species' functional significance for pest suppression. That is, communities dominated by large-bodied species exhibited, on average, greater predation rates. This result might be explained by increasing strength of per capita trophic interactions with body size (Berlow et al. 2009). Nevertheless, increasing the numerical dominance of large-bodied species was not, by itself, sufficient to explain the magnitude of pest suppression. Indeed, our study suggests that changes in the relative proportion of different size classes (i.e., body size frequency distributions) are also likely to alter the strength of top-down control. Specifically, we found that predation rates were highest in communities with even representation of small and large-bodied species compared to communities dominated by either large or small-bodied species. This might occur because individuals of different size classes interacted in fundamentally different ways which, in turn, influenced their collective impact on pest suppression. Competitive interactions among similar sized predators may lead to a decline in pest control provision (Dayan et al. 1990, Niemelä 1993, Gianuca et al. 2016). Conversely, a shift towards a more even size distribution is likely to promote species complementarity and elevate the level of pest control (Rudolf 2012, Ye et al.

2013). Though it is possible that increasing the size range of predators could promote intraguild predation as well (e.g., Krenek and Rudolf 2014), our work supports previous findings showing that increasing size diversity may enhance prey mortality despite the potential for antagonistic interactions among dissimilar sized predators (Rudolf 2012). In fact, different sized predators often differ to some extent in other traits such as microhabitat use and diel activity patterns (e.g., day versus night foragers) that may underpin differences in their exploitation of a shared prey (Rudolf 2006, Kamenova et al. 2015). In turn, these finer-scale niche differences among size classes may lead to relaxation of interspecific competition and, by extension, strengthen pest suppression through niche complementarity (Northfield et al. 2010). More symmetric body size distributions within a predator community thus might have consequences analogous to those of predator species evenness (Crowder et al. 2010). Consequently, the strength of pest suppression depends not only on the size of the dominant predators but is also strongly determined by the body size distribution of co-occurring species. This also implies that the performance of particular species is likely to be influenced by interactions with other predators in the community assemblage, not functional capacity alone.

The context dependency of species interactions may, at least in part, explain why variable outcomes in the interaction between predator diversity and pest control are often reported (Straub et al. 2008). Thus, while former studies already stressed the importance of targeting high-performing species (e.g., large-bodied species in our study) for achieving effective biological control (Straub and Snyder 2006, Long and Finke 2014), our analysis highlights that suboptimal species (i.e., small-bodied species) cannot be disregarded as they can strongly affect the performance of more efficient species and/or can drive different processes (e.g., complementarity) that contribute to an overall effect (see predation rates in Fig. 3.4c). As such, conservation strategies that only target a limited number of effective predators are not always an appropriate approach to promote pest suppression. Considering individual species in isolation when designing schemes to maintain agricultural biodiversity may be detrimental to other, important predators in the system, but also ultimately influence the performance to the very

species we are targeting to maximizing biocontrol. Further, relying on the performance of a few dominant predators undermines the resilience of the system, making it more susceptible to sudden environmental changes, and can translate into greater variability in pest control services over time (Macfadyen et al. 2011). Hence, for biological control to be maximized at the landscape scale and simultaneously for several pest species, the functional diversity of the predator community would have to be increased. In support of this view, we found that a shift towards a more diversified carabid community (in terms of body size distribution) resulted in stronger top-down control. This does not preclude the role of particular species being of key importance for effective pest suppression (i.e., species identity), especially in homogeneous landscapes where the high effectiveness of particular biocontrol agents has been linked to the simplified nature of the food web (Hawkins et al. 1999). Likewise, the presence of a particularly effective predator does not rule out the potential for positive or negative interactions among predators, as reported here.

Another important finding of this study is that body size alone does not explain the strength of top-down control. That is, the mere presence of a species with large body size did not always lead to increased pest control. Instead, our results show that species' food preferences can also influence their performance as biocontrol agents. Carnivorous species were largely responsible for top-down control (i.e., large species with increased abundance in simple landscapes, Fig. 3.3c), whereas herbivores and omnivores had little or no contribution. Although it might seem obvious that pest control was mainly driven by carnivorous species, this aspect is often ignored in studies examining the effects of body size on ecosystem functioning (Rudolf *et al.* 2014). Yet, we found clear evidence that similar-sized species (e.g., *Pterostichus* spp., *Harpalus* spp.) can have different diets, and accounting for this variation related to diet breadth may improve the capacity of body size as a predictor of pest control provision. Indeed, we show that although body size alone (i.e., CWM) explained a significant amount of the variance in predation rates ($R^2 = 0.57$), there is still substantial variation that remains to be explained. This is not surprising given that realized levels of pest control in natural communities depend on

numerous abiotic and biotic processes including interactions between multiple predators. This indicates that we need to consider other traits if we are to accurately predict how changes in predator body size influence the outcome of species interactions and the emergent impacts on pest suppression. Our results suggest that diet breadth is also an important underlying driver of species-based contributions to pest control, and it might help to explain why similar size predators differ in their relative contribution. Further research should also investigate the predictive capacity of body size when combined with other traits such as hunting mode and predator's microhabitat use that are well known to affect trophic interaction strengths (Schmitz 2007, Woodcock and Heard 2011). Despite obvious shortcomings of purely size-based approaches, our findings show that body size better predicted top-down control than other components of predator community structure (i.e., activity-density, species richness, and evenness), in accordance with previous work (Rusch et al. 2015, Gianuca et al. 2016).

In conclusion, our results show that landscape simplification influences the body size structure of ground beetle communities, with potential implications for pest control services. On the surface our results suggest that management strategies to maximize pest control should be aimed towards increasing predator body size by targeting specific species. However, changes in size distribution (i.e., skewness) within predator communities could also alter the strength of top-down control. Thus, communities with the same mean body size, but varying in the relative proportion of different size classes may have different effects on pest control. Given that both mean body size and size distributions are subject to landscape-driven variation, this suggests that there is no universal relationship between predator body size and pest control. Instead, our study shows that the relationship between predator body size and pest control is landscape-dependent and that the resulting magnitude of pest suppression is not always deducible from averaging body size of predators. Moreover, apart from body size, predator species differ in other traits like diet breadth, which may also affect the extent of pest regulation in a landscape-dependent manner given that different trophic groups vary in their sensitivity to land-use changes (Purtauf et al. 2005). Consequently, future schemes will need to adopt not only local practices to boost

populations of effective predators suited to specific pests, but also landscape management to sustain a carabid assemblage with a diverse set of traits to maximize overall pest suppression. In this regard, the adoption of practices such as low-impact tillage, reduced pesticide pressure, organic farming, and maintenance of non-crop refuges are promising management options that can be implemented at local and landscape scales to optimize pest control by ground beetles (Holland and Luff 2000, Landis et al. 2000).

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REFERENCES

- Andaloro, J. T., Rose, K. B., Shelton, A. M., Hoy, C. W., and Becker, R. F. 1983. Cabbage growth stages. *New York's Food and Life Sciences Bulletin* **101**: 1–4.
- Ball S. L., Woodcock B. A., Potts S. G., and Heard M. S. 2015. Size matters: body size determines functional responses of ground beetle interactions. *Basic and Applied Ecology* **16**: 621–628.
- Balvanera, P., Kremen, C., and Martínez-Ramos, M. 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecological Applications* **15**: 360–375.
- Berlow, E. L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R. J., and Brose, U. 2009. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 187–191.
- Birgé, L., and Rozenholc Y. 2006. How many bins should be put in a regular histogram. *ESAIM: Probability and Statistics* **10**: 24-45.
- Bousquet, Y. 2010. Illustrated Identification Guide to Adults and Larvae of Northeastern North American Ground Beetles (Coleoptera: Carabidae). Sofia-Moscow, Bulgaria: Pensoft Publishers.
- Bousquet, Y., and Larochele, A. 1993. Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America North of Mexico. *Memoirs of the Entomological Society of Canada* **167**: 1-397
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed.). New York, NY, USA: Springer-Verlag New York.
- Cadotte, M.W., Carscadden, K., and Mirotnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**: 1079-1087.
- Cardinale B.J, Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., ... Naeem, S.

2012. Biodiversity loss and its impact on humanity. *Nature* **486**: 59–67.
- Clare, D.S., Spencer, M., Robinson, L.A., and Frid, C.L.J. 2016. Species-specific effects on ecosystem functioning can be altered by interspecific interactions. *PLoS ONE* **11**: e0165739.
- Clark, M.S., Gage, S.H., and Spence, J.R. 1997. Habitat and management associated with common ground beetles (Coleoptera: Carabidae) in a Michigan agricultural landscape. *Environmental Entomology* **26**: 519–527.
- Cohen, J.E., Pimm, S.L., Yodzis, P., and Saldana, J. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* **62**: 67–78.
- Crowder, D.W., Northfield, T.D., Strand, M.R., and Snyder, W.E. 2010. Organic agriculture promotes evenness and natural pest control. *Nature* **466**: 109–112.
- Davenport J.M., and Chalcraft, D.R. 2013. Nonconsumptive effects in a multiple predator system reduce the foraging efficiency of a keystone predator. *Ecology and Evolution* **3**: 3063–3072.
- Dayan, T., Simberloff, D., Tchernov, E., and Yomtov, Y. 1990. Feline canines: community-wide character displacement among the small cats of Israel. *American Naturalist* **136**: 39–60.
- Díaz, S., Purvis, A., Cornelissen, J.H., Mace, G.M., Donoghue, M.J., Ewers, R.M., ... Pearse, W.D. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**: 2958–2975.
- Doledec, S., Chessel, D., and Gimaret-Carpentier, C. 2000. Niche separation in community analysis: a new method. *Ecology* **81**: 2914–2927.
- Dray, S., and Dufour, AB. 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software* **22**: 1–20.
- Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., ... Westphal, C. 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications* **6**: 8568.
- Gaüzère, P., Doucier, G., Devictor, V., and Kéfi, S. 2019. A framework for estimating species-specific contributions to community indicators. *Ecological Indicators* **99**: 74–82.

- Gianuca, A.T., Pantel, J.H., and De Meester, L. 2016. Disentangling the effect of body size and phylogenetic distances on zooplankton top-down control of algae. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20160487.
- Greenop, A., Woodcock, B.A., Wilby, A., Cook, S., and Pywell, R.F. 2018. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology* **99**: 1771–1782.
- Griffin, J.N., Byrnes, J.E., and Cardinale, B.J. 2013. Effects of predator richness on prey suppression: a meta-analysis. *Ecology* **94**: 2180–2187.
- Hanson, H., Palmu, E., Kirkhofer, K., Smith, H.G., and Hedlund, K. 2016. Agricultural Land Use Determines the Trait Composition of Ground Beetle Communities. *PLoS ONE* **11**: e0146329.
- Hawkins, B.A., Mills, N.J., Jervis, M.A., and Price, P.W. 1999. Is the biological control of insects a natural phenomenon? *Oikos* **86**: 493–506.
- Holland, J.M., and Luff, M.L. 2000. The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Reviews* **5**: 109–129.
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., and Assmann, T. 2013. Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity* **7**: 195–205.
- Honêk A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* **66**: 483-492.
- Jenkins, D. G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R., ... Williams, S.E. 2007. Does size matter for dispersal distance? *Global Ecology and Biogeography* **16**: 415–425.
- Jonsson, T., Kaartinen, R., Jonsson, M., and Bommarco, R. 2018. Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters* **21**: 702–712.
- Juliano, S.A. 1986. Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). *Ecology* **67**: 1036-1045.

- Kamenova, S., Tougeron, K., Cateine, M., Marie, A., and Plantegenest, M. 2015. Behaviour-driven micro-scale niche differentiation in carabid beetles. *Entomologia Experimentalis et Applicata* **155**: 39-46.
- Kotze, D.J., and O'Hara, R.B. 2003. Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* **135**: 138– 148.
- Krenek, L., and Rudolf, V.H. 2014. Allometric scaling of indirect effects: body size ratios predict non-consumptive effects in multi-predator systems. *Journal of Animal Ecology* **83**: 1461–1468.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment* **74**: 187–228.
- Laliberté, E., Legendre, P., and Shipley, B. 2015. FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R package version 1.0-12.
- Landis, D.A., Wratten, S.D., and Gurr, G.M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* **45**: 175–201.
- Lindroth, C. H. 1961. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica Supplementum*, **20**: 1-200.
- Lindroth, C. H. 1963a. The fauna history of Newfoundland illustrated by carabid beetles. *Opuscula Entomologica Supplementum* **23**: 1-112.
- Lindroth, C. H. 1963b. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica Supplementum* **24**: 201-408.
- Lindroth, C. H. 1966. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica Supplementum* **29**: 409-648.
- Lindroth, C. H. 1968. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica Supplementum* **33**: 649-944.
- Long, E.Y., and Finke, D.L. 2014. Contribution of predator identity to the suppression of herbivores by a diverse predator assemblage. *Environmental Entomology* **43**: 569–576.

- Lövei, G. L., and Sunderland, K. D. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**: 231–256.
- Macfadyen, S., Craze, P.G., Polaszek, A., van Achterberg, K., and Memmott, J. 2011. Parasitoid diversity reduces the variability in pest control services across time on farms. *Proceedings of the Royal Society B: Biological Sciences* **278**: 3387–3394.
- Martin, E. A., Reineking, B., Seo, B., and Steffan-Dewenter I. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes *Proceedings of the National Academy of Sciences of the United States of America* **110**: 5534–9.
- Menalled, F., Lee, J.C., and Landis, D. 1999. Manipulating carabid beetle abundance alters prey removal rates in corn fields. *BioControl* **43**: 441-456.
- Nelemans, M.N.E. 1987. On the life-history of the carabid beetle *Nebria brevicollis* (F.). *Netherlands Journal of Zoology* **37**: 26-42.
- Niemelä, J. 1993. Interspecific Competition in Ground-Beetle Assemblages (Carabidae): What Have We Learned? *Oikos*, **66**: 325-335.
- Northfield, T.D., Snyder, G.B., Ives, A.R., and Snyder, W.E. 2010. Niche saturation reveals resource partitioning among consumers. *Ecology Letters* **13**: 338-348.
- Perović, D. J., Gámez-Virués, S., Landis, D. A., Wäckers, F., Gurr, G. M., Wratten, S. D., ... Desneux, N. 2017. Managing biological control services through multi-trophic trait interactions: Review and guidelines for implementation at local and landscape scales. *Biological Reviews* **93**: 306– 321.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge: Cambridge University Press.
- Pinheiro, J. C., and Bates, D. M. 2000. Mixed effects models in S and S-Plus. New York, NY, USA: Springer-Verlag New York.
- Prasad, R.P., and Snyder, W.E. 2004. Predator interference limits fly egg biological control by a guild of ground-active beetles. *Biological Control* **31**: 428–437.
- Purtauf, T., Dauber, J., and Wolters, V. 2005. The response of carabids to landscape

- simplification differs between trophic groups. *Oecologia* **142**: 458–464.
- Rand, T. A., and Tschardtke, T. 2007. Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos* **116**: 1353–1362.
- Rouabah, A, Lasserre-Joulin, F., Amiaud, B., and Plantureux, S. 2014. Emergent effects of ground beetles size diversity on the strength of prey suppression. *Ecological Entomology* **39**: 47-57.
- Rudolf, V. H. W. 2006. The influence of size-specific indirect interactions in predator-prey system. *Ecology* **87**: 362-371.
- Rudolf, V. 2012. Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator-prey systems. *Journal of Animal Ecology* **81**: 524–532.
- Rudolf, V. H. W., Rasmussen, N. L., Dibble, C. J., and Van Allen, B. G. 2014. Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20133203.
- Rusch, A., Binet, D., Delbac, L., and Thiéry, D. 2016. Local and landscape effects of agricultural intensification on Carabid community structure and weed seed predation in a perennial cropping system. *Landscape Ecology* **31**: 2163–2174.
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., and Ekbom, B. 2014. Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia* **175**: 971–983
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., and Ekbom, B. 2015. Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology* **16**: 250–259.
- Russell, M.C., Lambrinos, J., Records, E., and Ellen, G. 2017. Seasonal shifts in ground beetle (Coleoptera: Carabidae) species and functional composition maintain prey consumption in Western Oregon agricultural landscapes. *Biological Control* **106**: 54–63.
- Schmitz, O.J. (2007). Predator diversity and trophic interactions. *Ecology* **88**: 2415–2426.
- Shelton, A. M., Cooley, R. J., Kroening, M. K., Wisely, W. T., and Eigenbrode, S. D. 1991.

- Comparative analysis of two rearing procedures for diamondback moth (Lepidoptera: Plutellidae). *Journal of Entomological Science* **26**: 17–26.
- Sih, A., Englund, G., Wooster, D. 1998. *Trends in Ecology and Evolution* **13**: 350–355.
- Straub, C.S., Finke, D.L., and Snyder, W.E. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals?. *Biological Control* **45**: 225–237.
- Straub, C.S., and Snyder, W.E. 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology* **87**: 277–282.
- Suenaga, H., and Hamamura, T. 2001. Occurrence of carabid beetles (Coleoptera: Carabidae) in cabbage fields and their possible impact on lepidopteran pests. *Applied Entomology and Zoology* **36**: 151–160.
- Tolkinen, M., Mykrä, H., Markkola, A-M., Aisala, H., Vuori, K.M., Lumme, J., ... Muotka, T. 2013. Decomposer communities in human-impacted streams: Species dominance rather than richness affects leaf decomposition. *Journal of Applied Ecology* **50**: 1142–1151.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters* **8**: 857–874.
- Tsiafouli, M.A., Thebault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten. W.H, Birkhofer. K., ... Hedlund, K. 2015. Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology* **21**: 973–985.
- USDA, National Agricultural Statistics Service. 2016. New York cropland data layer (2014-15 ed.). USDA-NASS, Washington, D.C, USA. <https://nassgeodata.gmu.edu/CropScape/>
- Winfree, R., Fox, J. W., Williams, N.M., Reilly, J.R., and Cariveau, D.P. 2015 Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* **18**: 626–635.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., ... Bommarco, R. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology* **48**:

570–579.

- Woodcock, B.A., and Heard, M.S. 2011. Disentangling the effects of predator hunting mode and habitat domain on the top-down control of insect herbivores. *Journal of Animal Ecology* **80**: 495-503.
- Woodward, G., and Hildrew, A.G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* **71**: 1063–1074.
- Ye, L., Chang, C.-Y., Garcia-Comas, C., Gong, G.-C., and Hsieh, C.-H. 2013. Increasing zooplankton size diversity enhances the strength of top-down control on phytoplankton through diet niche partitioning. *Journal of Animal Ecology* **82**: 1052–1060.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York, NY, USA: Springer-Verlag New York.

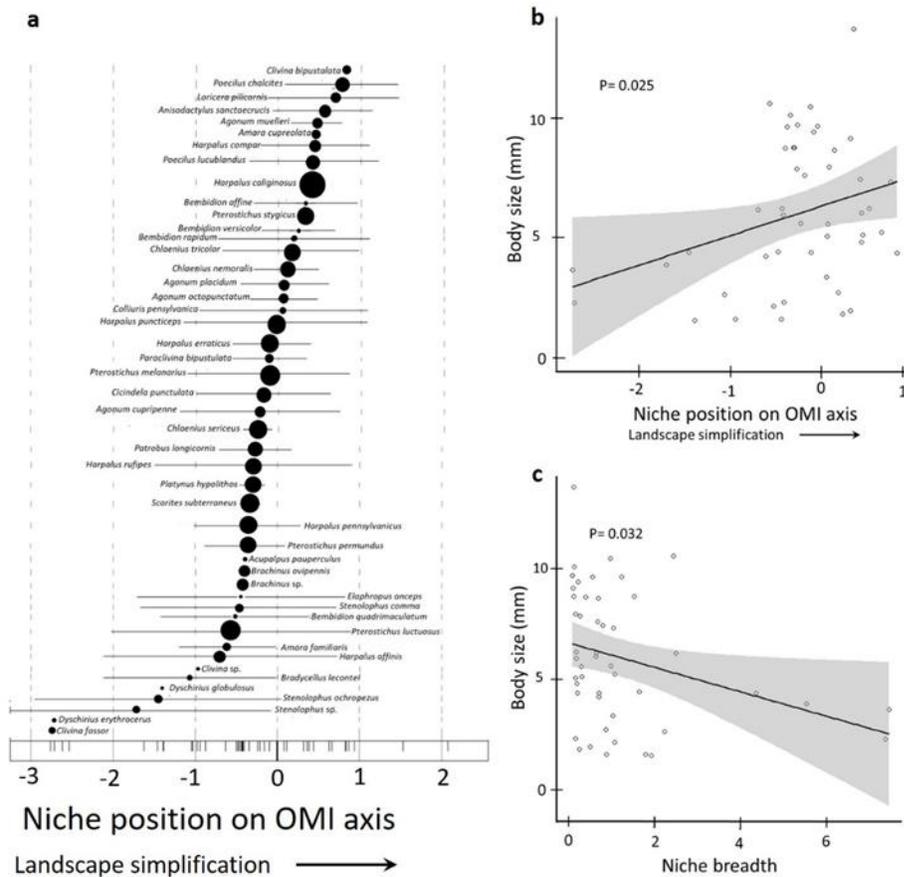


Fig. 3.1. **a.** Species niche position and niche breadth for all carabid species along the landscape simplification gradient. This analysis was based on the Outlying Mean Index (OMI). Circles represent the average position along the landscape gradient used by every species and the horizontal bars correspond to $\pm 1SD$ as a measure of niche breath. Values near zero indicate proportion of agriculture near the available mean for the study region (i.e. ~30%), whereas values far from this origin indicate marginal environments, that is, complex (negative values) or simple (positive values) landscapes. Small vertical bars at the bottom of the panel correspond to the position of the experimental plots. The size of the circles is proportional to the relative body size of each species. **b.** Relationship between species body size and landscape niche position (outlying mean index). **c.** Relationship between species body size and niche breadth along the gradient of landscape simplification. Regression lines and 95% confidence intervals shown.

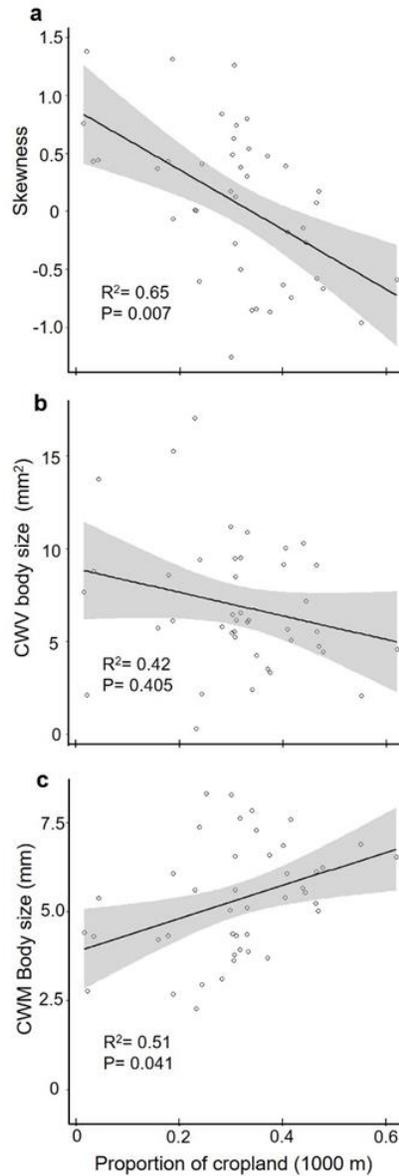


Fig. 3.2. Relationships between the proportion of cropland in a 1000 m radius around the experimental plots and (a) skewness coefficients of body size distribution, (b) community weighted variance of body size (CWV), and (c) community weighted mean body size (CWM). Each data point represents a single community (plot). Positive and negative skewness indicate dominance by species with small and large-bodied size, respectively. Lines depict predicted trends from linear mixed-effects models and associated 95% confidence intervals (gray shaded). Conditional coefficient of determination (R^2) and significance of fixed effects are shown.

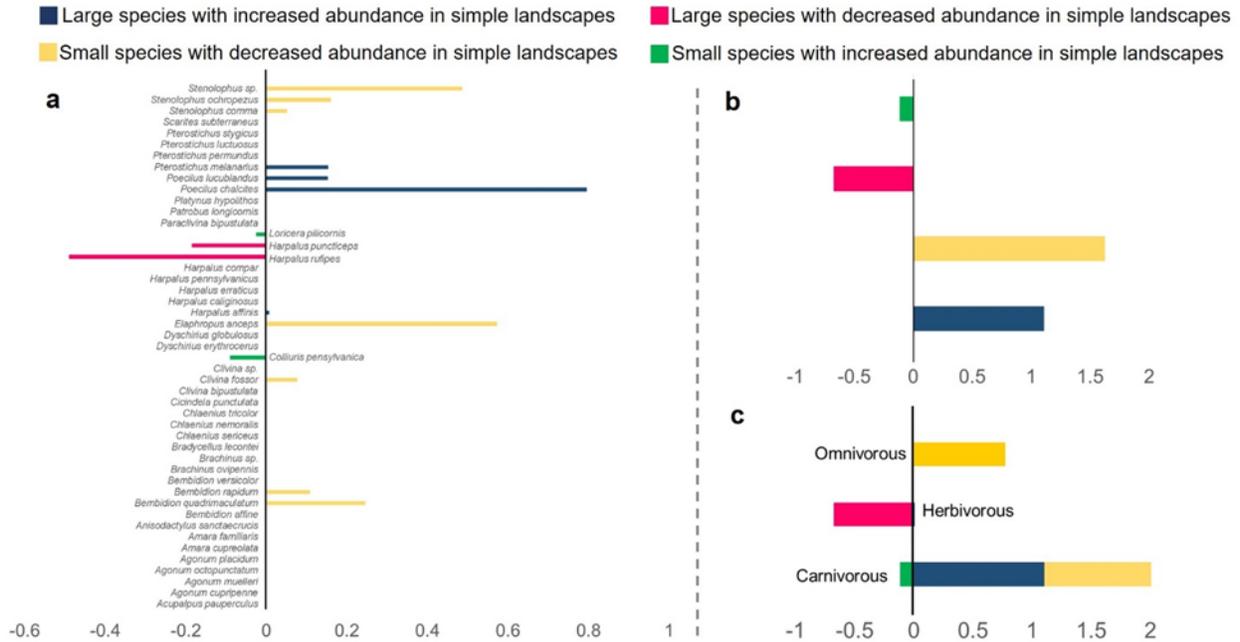


Fig 3.3. a. Species-specific contributions to community weighted mean (CWM) shifts in body size along the landscape simplification gradient. A positively contributing species tends to increase CWM along the landscape simplification gradient whereas negatively contributing species tends to decrease it. Species positively contributing are shown on the right side and negatively contributing species on the left side. Bar colors indicate the interaction between size category (i.e., small vs. large) and population trend (i.e., increased vs. decreased abundance along the landscape gradient). **b.** Cumulative contribution by size category and population trend. **c.** Cumulative contributions by trophic group.

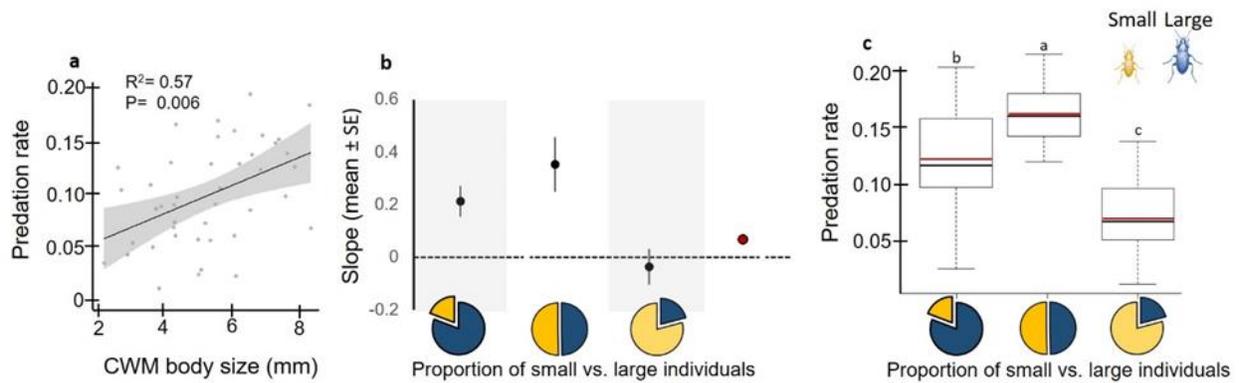


Fig 3.4. a. Relationship between community weighted mean body size (CWM) and predation rates on sentinel diamondback moth pupae in the field. Line depicts predicted trend from the linear mixed-effects model and associated 95% confidence intervals (gray shaded). Conditional coefficients of determination (R^2) and significance of fixed effects are shown. **b.** Slopes of the CWM body size-predation relationships in communities with different patterns of body size distribution: left-skewed (communities dominated by large-bodied species), symmetric (similar number of small and large species), and right-skewed (communities dominated by small-bodied species). Overall mean slope for the whole community in red. **c.** Boxplots of predation rates for communities with different patterns of body size distribution (sample sizes are: left-skewed = 11, symmetric = 12, and right-skewed = 19). Lines within each box represent the median (black) and mean (red) values. Box plot whiskers extend to 1.5 times the interquartile range. Different letters above boxplots indicate significant differences between groups (one-way ANOVA followed by a Tukey HSD test, $P < 0.05$).

CHAPTER FOUR

LANDSCAPES OF FEAR: HOW LANDSCAPE COMPOSITION INFLUENCES THE MAGNITUDE OF ANTIPREDATOR RESPONSES IN AN AGRICULTURAL INSECT PEST

Abstract

Prey organisms often respond to the risk of predation by altering behavioral, physiological, and morphological traits. These antipredator responses increase prey survival, but often come at a cost of reduced feeding and/or reproduction rates, which ultimately may lower prey populations with cascading benefits for plant production. Although such antipredator responses have been relatively well studied in small-scale microcosm environments, they remain largely unexplored for plant-arthropod communities in heterogeneous agricultural landscapes. Here, we examined how variation in predator abundance across a gradient of landscape complexity influences antipredator responses of a major agricultural pest, the Colorado potato beetle (*Leptinotarsa decemlineata*). Within the study region (New York State, USA) pest populations were collected in 19 potato fields encompassing a 20-fold natural difference in predator abundance. For each pest population, we measured two behavioral larval responses to the risk of predation: leaf feeding and intra-clutch cannibalism. Using laboratory trials with stink bug predators (*Podisus maculiventris*) that were surgically manipulated so they could hunt but not kill, we also tested the magnitude of antipredator responses among pest populations. We showed that predator abundance was higher in agriculturally dominated landscapes (i.e., simple landscapes). Furthermore, pest populations from simple landscapes exhibited significantly higher levels of intra-clutch cannibalism and lower plant feeding, behaviors known to reduce the likelihood of being predated. Results from the lab experiment with non-lethal predators further confirm that antipredator responses were stronger in simple than in complex landscapes. Thus, our findings provide empirical evidence that landscape-level variation in predation risk is associated with behavioral changes among population of *L. decemlineata*. A greater understanding of these indirect landscape effects on pest regulation is necessary to fully explore the range of mechanisms by which biological control could be strengthened in agroecosystems.

Key words: biological pest control; landscape of fear; *Leptinotarsa decemlineata*; non-consumptive effects; predation risk; *Solanum tuberosum*.

INTRODUCTION

Predators provide important ecosystem services and functions such as the control of economically important agronomic pests (Finke and Snyder 2010). Such a reduction in pest pressure can occur directly by removing prey through consumption, or by indirect non-consumptive effects associated with changes in a prey's behavior to reduce predation risk (Lima 1998). Because these changes in prey behavior often come at the cost of reduced food intake with subsequent impacts on key demographic parameters such as growth rate, survival and/or reproduction (Schmitz 1998), non-consumptive effects could be as important as actual predation for biocontrol (Preisser et al. 2005). However, relative to the large body of literature exploring the consequences of direct consumption (Griffin et al. 2013), very few studies have examined the importance of non-consumptive effects on pest suppression. Recent syntheses have, however, shown that non-consumptive effects are widespread within arthropod communities and may potentially lead to strong cascading effects that benefit plants (Buchanan et al. 2017, Hermann and Landis 2017). What is lacking is empirical evidence on whether non-consumptive effects indeed influence insect pests under open-field conditions and across heterogeneous landscapes.

Most of our understanding of non-consumptive effects in agricultural systems comes from studies performed in laboratory settings (Hermann and Landis 2017). Although these studies provide valuable insights that elucidate the potential mechanisms at work (Thaler et al. 2012, Hermann and Thaler 2014), it is unclear whether these studies reflect the reality of what occurs in the field across spatially heterogeneous landscapes. At larger spatial scales, the landscape composition surrounding crop fields is highly variable, ranging from homogeneous landscapes dominated by agriculture, to heterogeneous landscapes where agricultural land is interspersed with natural habitats (i.e., forest, meadows, and shrubland). This spatial heterogeneity can cause marked changes in the abundance of predator assemblages, with predators usually being more abundant in landscapes with a greater proportion of natural habitats

(Chaplin-Kramer 2011). Because predator abundance and the concomitant magnitude of predation risk can change across landscape gradients, it follows that prey species must be able to adapt their responses to changes in the risk environment. The importance of predation risk in generating variable landscapes of fear that shape prey antipredator responses has long been recognized in studies with vertebrates (Laundré et al. 2001), yet it remains to be examined empirically in arthropod predator-prey systems.

In this study, we examined responses to predation risk in the specialist potato pest, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). Previous work has shown that *L. decemlineata* (the Colorado potato beetle, hereafter CPB) can respond to the risk of predation through phenotypically plastic responses, including behavioral, physiological, and life history trait changes (Kaplan et al. 2014, Tigreros et al. 2017). Perhaps the most commonly occurring form of predator avoidance in this species involves reduced plant consumption, because foraging activity increases vulnerability to predation (Pfannenstiel et al. 1995). Another behavior that can help CPB overcome challenging environments, such as those under the threat of predators, is intra-clutch cannibalism (Tigreros et al. 2017). When facing the risk of predation, parents improve their offspring's chances of survival by promoting intra-clutch cannibalism (Tigreros et al. 2017). Consuming eggs within the natal clutch then reduces the need of larvae to search for food, thus decreasing the risk of predation during the most vulnerable lifecycle stage. Indeed, reduction in feeding in response to predation risk decreases the likelihood of CPB larvae being predated by up to 30% (Tigreros et al. 2017). Importantly, these adaptative responses to the risk of predation may occur through contemporary experience with predator cues, or through legacies of past experiences with predators, whether their own or those of their mothers.

Predation risk is not, however, the only selective force shaping trait variation among prey populations as the availability of food is also an important factor determining phenotypic responses in field conditions. For example, body size is strongly determined by the availability of resources and their distribution across space (Hillaert 2018). With land-use changes, the spatial distribution of crop-food resources is altered, and therefore expected to exert strong selection on

body size (Gámez-Virués et al. 2015, Renauld et al. 2016). Body size variation may in turn determine the magnitude of antipredator responses (Preisser and Orrock 2012). For example, larger or better-fed organisms are more likely to exhibit stronger responses to predation risk by reducing feeding or producing offspring with greater antipredator behaviors (Lima and Dill 1990, Tigreros et al. 2018). Alternatively, larger body size may increase the likelihood of detection and attack by predators (McClure and Despland 2011), which in turn could elicit a selection towards smaller body size (Bell et al. 2011). Consequently, landscape-scale effects on body size and predation risk are not mutually exclusive, but rather operate simultaneously and interactively to shape antipredator responses.

Here, we examined the influence of landscape composition on prey responses to predation risk. Specifically, we asked: (1) does landscape composition influence prey responses to predators?, and (2) whether predator abundance or prey body size drive the magnitude of these anti-predator responses.

MATERIALS AND METHODS

Sampling of CPB and its naturally occurring predators

We collected *L. decemlineata* from 19 commercial potato farms (*Solanum tuberosum*) in central New York (USA) during 2016. These farms were separated from each other by at least 3 km. Adult CPB beetles and egg masses were hand collected from five randomly selected locations at each farm. Sampling occurred in mid-June and late July, which represent the overwintering and summer generations of CPB in the study region, respectively.

Abundance of naturally occurring predators was recorded using yellow sticky cards (15 × 30 cm, BioQuip, Rancho Dominguez, CA, USA). At each farm, two yellow sticky cards were placed within the field at about the height of the plant canopy. These traps were collected biweekly from June to August capturing the periods when CPB are most active. Although the community of natural enemies in New York potato fields is composed of a diverse assemblage of generalist predators, our sampling focused on ladybird beetles because they were the most

abundant predatory group across sites (R. Perez-Alvarez, personal observation). Ladybird beetles prey extensively on CPB eggs and small larvae and can significantly reduce CPB population in the field (Hough-Goldstein et al. 1993).

Landscape composition

To quantify the landscape composition surrounding sampled *L. decemlineata* populations, we created land-cover maps that encompassed all areas within 1500-m radius of each site using data from the National Agricultural Statistics Service (USDA-NASS 2017) and spatial statistic tools in ArcGIS 10.3. We then calculated the proportion of natural habitats (forests, shrublands, woody wetlands, and meadows) and cropland around each site at three scales: 500 m, 1000 m, and 1500. We chose the 1500-m scale as our maximum because it is the longest dispersal distance documented for *L. decemlineata* (Weisz et al. 1996).

Landscape variation in intra-clutch cannibalism

To examine intra-clutch cannibalism, egg masses collected from field populations were placed into separated petri dishes (2.5 cm in diameter) lined with moistened paper towels. We examined egg masses daily for up to 7 days after hatching and registered the number of unhatched eggs, larvae, and missing eggs. In all cases, we eliminated hunger as the primary driver of cannibalism by daily adding fresh potato foliage to the petri dishes. Proportion of eggs cannibalized was then calculated dividing the number of eggs missing by the initial number of eggs in a given mass. Number of egg masses examined per farm varied between 6 and 15 based on availability of clutches in the field.

Landscape variation in body size

Fifteen males and fifteen female adults from each field population were randomly chosen to measure body size. Body size (i.e., the distance from the anterior margin of the clypeus to the elytral apex) was digitally measured for all selected specimens using an Olympus SZX10 stereomicroscope connected to a computer installed with the micro imaging software cellSens (Olympus Corp., Tokyo, Japan). Only females were included in subsequent analyses because no consistent patterns were found with males.

Landscape variation in leaf consumption

Five to ten pairs of adult beetles from each field population were allowed to mate and then females were allowed to oviposit on potted potato plants in the laboratory (cv. Yukon Gold). Egg masses from these populations were removed from the plants and incubated at 25°C and a photoperiod of 16:8 (L:D). After hatching (< 12h old), a single neonate was placed into a petri dish (3.5 cm in diameter) provided with a potato leaf disk (cv. Yukon Gold and 2.5 cm in diameter) that was placed in a thin layer of agar (2% wt/vol), so that the abaxial side of the leaf was in contact with the agar to provide moisture and support to the leaf tissue. After 3 days of ad libitum feeding at 25°C and 16L: 8D, the leaf area eaten (mm²) for each larva was digitally quantified using ImageJ. For each population, a total of five to ten larvae from different females were tested.

Landscape effects on prey responses to predation risk

To test the effect of landscape composition on prey responses to predation risk, egg masses from each field populations were collected as outlined above. Neonates from the same egg mass were individually weighted and enclosed into a 266 mL cup with a potato leaflet, and randomly allocated into two treatments: control or predation risk. A complete description of the methods to manipulate predation risk is presented elsewhere (Tigreros et al. 2017, 2018). In short, we created ‘risk-predators’ by surgically removing the terminal 1-mm segment of the stylet of adults of stink bug predators (*Podisus maculiventris*). Previous work showed that these surgically altered stink bugs are unable to kill the beetle larva, but their foraging behavior does not differ from that of their unaltered counterparts (Kaplan and Thaler 2010).

For the cups assigned to the predator risk treatment, a single ‘risk-predator’ was introduced and kept at 25°C and 16L: 8D h. No predators were released in the control cups. After 3 days, leaf consumption for larvae in the two treatments was digitally quantified using ImageJ. For each field populations, treatments (i.e., presence vs. absence of stink bugs) were replicated between three to six times from egg masses laid by different females.

Statistical Analyses

A multilevel path analysis approach (Shipley 2009) was used to test the direct and indirect effects of landscape composition on intra-clutch cannibalism and leaf consumption. Each path analysis was developed from a set of mixed-effect models as follows. First, linear (lme) and generalized mixed effect models (glmer) were used to examine the effects of landscape composition, predator abundance, and CPB female body size on the rates of cannibalism and leaf consumption. A binomial error structure was used to model rates of cannibalism and a gaussian error structure was used for leaf consumption. In the cannibalism model, the response variable was defined as the number of eggs cannibalized versus the number of non-cannibalized eggs per egg mass, and egg mass size was used as an offset variable. Leaf consumption was square-root transformed to meet model assumptions (normality and homoscedasticity). Landscape composition was defined as either the proportion of cropland or the proportion of natural areas as both variables were highly correlated at all scales (Spearman's $r_s < -0.45$, $P < 0.001$ at all scales). Different spatial scales (i.e., 500, 1000, and 1500-m) were analyzed separately. In this and every subsequent analyses we restricted our interpretation to the one land cover and spatial scale in which landscape predictors explained the most variation (see Appendix 1 for a list of the models). Second, predator abundance and CPB female body size were included as response variables in separate models with landscape composition as a fixed effect. Thus, path models considered the direct effects of landscape composition on the rates of cannibalism and leaf consumption, along with indirect effects via predator abundance and female body size. Random effects in all models included "farm identity" and generation (i.e., overwintering or summer) to account for differences across sites and seasons. Prior analysis, models were tested for collinearity and spatial autocorrelation. No significant collinearity (VIF scores were < 1.5) or spatial correlation ($0.06 < r < 0.08$, $P > 0.240$) were detected for any model. The overall fit of each path model was then tested using a Fisher's C statistics. We further improve model fit by removing or adding significant relationships ($P < 0.05$), and reassessing AIC values. Path models with the smallest AIC values were considered to better fit the data (Burnham and Anderson

2002). After choosing the best-fitting models, path coefficients were standardized by mean and variance to enable the comparison of the relative importance of different predictors.

To test the effects of landscape composition on the responses to predation risk, we used a linear mixed-effect model (lme). Response variable was defined as area of leaf consumed (square-root transformed), and larval initial weight (μg) was used as an offset variable. Fixed factors included treatment (presence or absence of stink bug-induced predation risk), landscape composition, and the treatment by landscape interaction. Random effects included “farm identity”, generation (i.e., overwinter or summer), and “female sting bug identity”. The model conformed lme assumptions (i.e. normality, heteroscedasticity) and did not display evidence of collinearity (variance inflation factors < 2.5 ; Zuur et al. 2009) or spatial autocorrelation ($0.06 < r < 0.08$, $P > 0.240$). To assess the significance of fixed effects, we compared nested models with likelihood ratio tests (Zuur et al. 2009). In a second step, we performed preplanned contrasts to determine whether mean differences between the predator risk treatment and the control were contingent on the composition of the surrounding landscape. Pairwise multiple comparisons of the marginal means were calculated using a Tukey adjustment for an overall error rate of 0.05 (Lenth et al. 2018). All statistical analyses were conducted using lme4 (Bates et al. 2015) nlme (Pinheiro et al. 2015), piecewiseSEM (Lefcheck 2016), and emmeans (Lenth et al. 2018) packages in R v.3.5.3 (R Development Core Team, 2019).

RESULTS

Both the cannibalism and leaf consumption path models provided a good fit to the data (cannibalism: Fisher’s $C = 7.3$, $df = 4$, $P = 0.121$; leaf consumption: Fisher’s $C = 5.74$, $df = 4$, $P = 0.219$) (Figs. 1a-b). We found no evidence that landscape composition directly influenced the rates of cannibalism or leaf consumption among CPB populations. Rather, we showed that cannibalism and leaf consumption were determined by indirect effects mediated by changes in predator abundance and CPB female body size across the landscape gradient. Predator abundance was negatively associated with the proportion of natural habitats at 1500-m radius surrounding each potato field ($P = 0.042$, Fig. 2a). Similarly, CPB female body size was

negatively associated with proportion of natural habitats at 1500-m ($P = 0.025$, Fig. 2b). Thus, predator abundance and CPB female size decreased by 70% and 9%, respectively, in landscapes containing high proportion of natural habitats (i.e., complex landscapes) compared with simple landscapes.

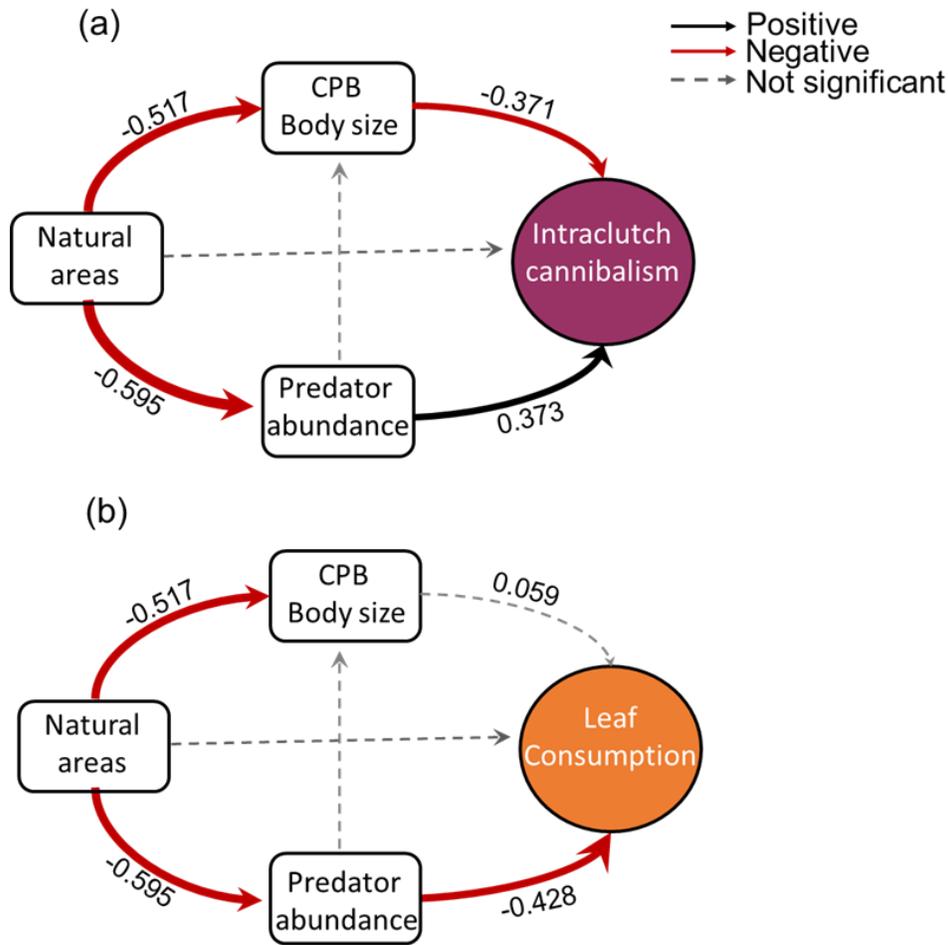


Fig. 1. Path analyses showing the relationships between proportion of natural areas (1500 m radius), predator abundance, CPB female body size, and the rates of cannibalism (a) and leaf consumption (b). Black, red and dash arrows represent positive, negative and non-significant paths ($P > 0.05$), respectively. The number along the arrows are standardized path coefficients obtained from mixed-effect models. The width of each arrow is proportional to the strength of the relationship.

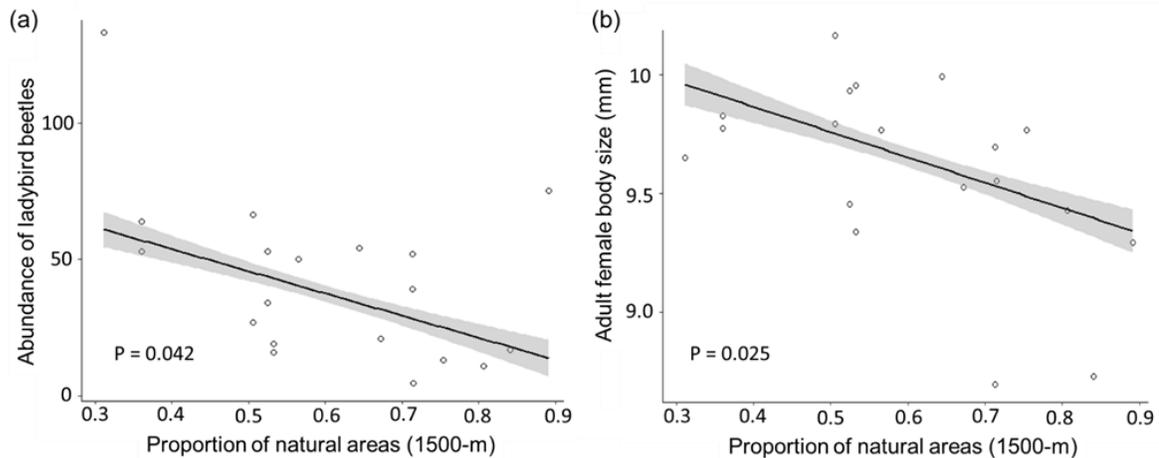


Fig. 2. Relationship between the proportion of natural areas in the surrounding landscape at a 1500-m radius and predator abundance (a) and CPB female body size (b). Each data point represents mean values for a single field population (farm). Lines indicate predicted trends and associated 95% confidence intervals (gray shaded).

Further, we found that predator abundance and CPB female body size directly affected the rates of cannibalism (Fig. 3). There was a positive relationship between the rates of cannibalism and the abundance of predators ($P = 0.005$, Fig. 3a), but negative relationship of cannibalism with female body size ($P = 0.003$, Fig. 3b). Contrary to the results for cannibalism, leaf consumption was strongly and negatively related to predator abundance ($P = 0.004$, Fig. 3c), whereas female body size did not significantly predict leaf consumption ($P = 0.484$, Fig. 3d). We detected no significant relationship between predator abundance and CPB female body size ($P > 0.4$, Figs. 1a-b).

In the predation risk experiment, we observed a significant effect of predator presence on leaf consumption ($F_{1,366} = 6.022$, $P = 0.015$; Fig. 4). Larvae from the same egg mass exposed to a predator consumed on average 13% less leaf area relative to predator-free controls. The magnitude of CPB leaf area consumption responses to predator exposure was influenced by the composition of the surrounding landscape. We found a significant interaction between the proportion of cropland at the 500-m scale and predation risk whereby the influence of predators

became progressively stronger with increasing proportion of cropland in the landscape ($F_{1,366} = 3.940$, $P = 0.048$; Fig. 4 a-b). Indeed, larvae from simple landscapes (i.e., crop-dominated landscapes) consumed 23% less foliage when exposed to predators compared with the control (Fig. 4b). In contrast, in complex landscapes there were no differences in leaf consumption between control and predation risk treatments (Fig. 4b).

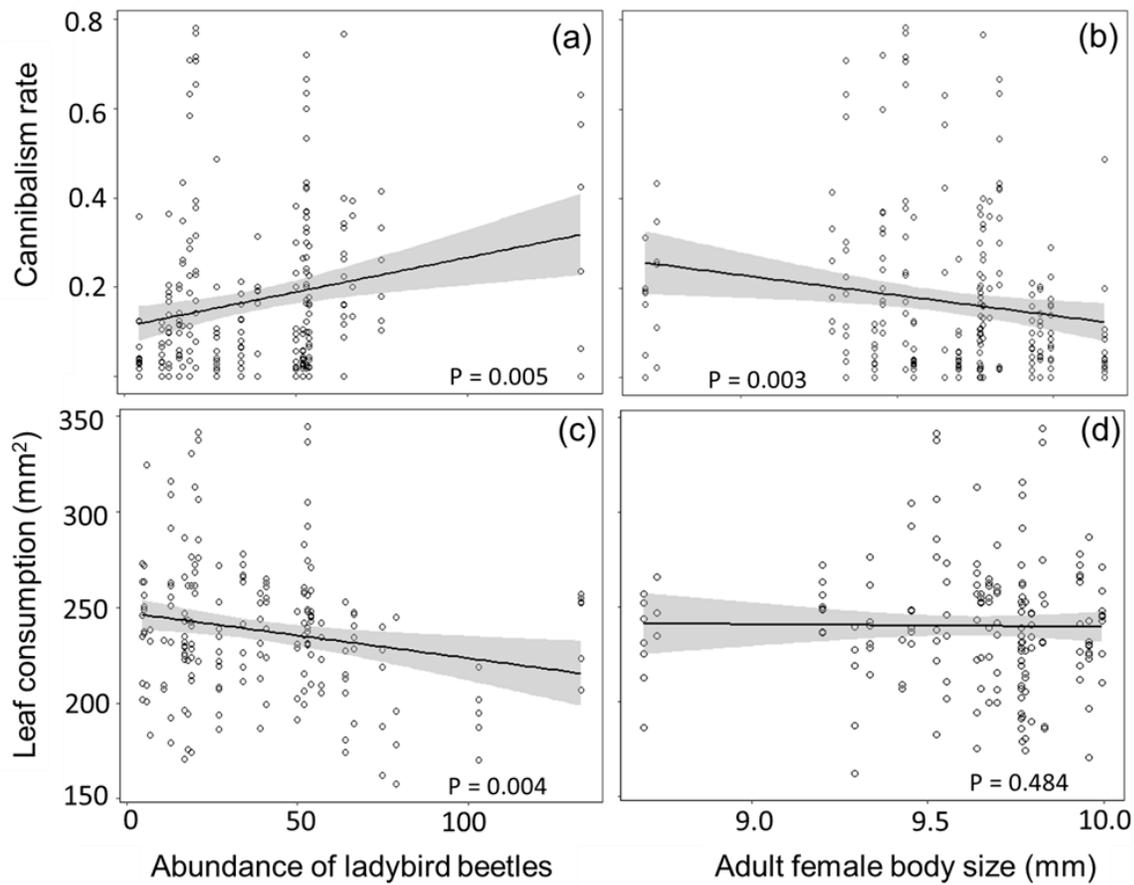


Fig. 3. Effects of predator abundance and CPB female body size on the rates of intra-clutch cannibalism (a-b) and leaf consumption (c-d) of CPB larvae. Each data point represents values of a single egg mass (a-b) or a single larva (c-d). Lines indicate predicted trends and associated 95% confidence intervals (gray shaded).

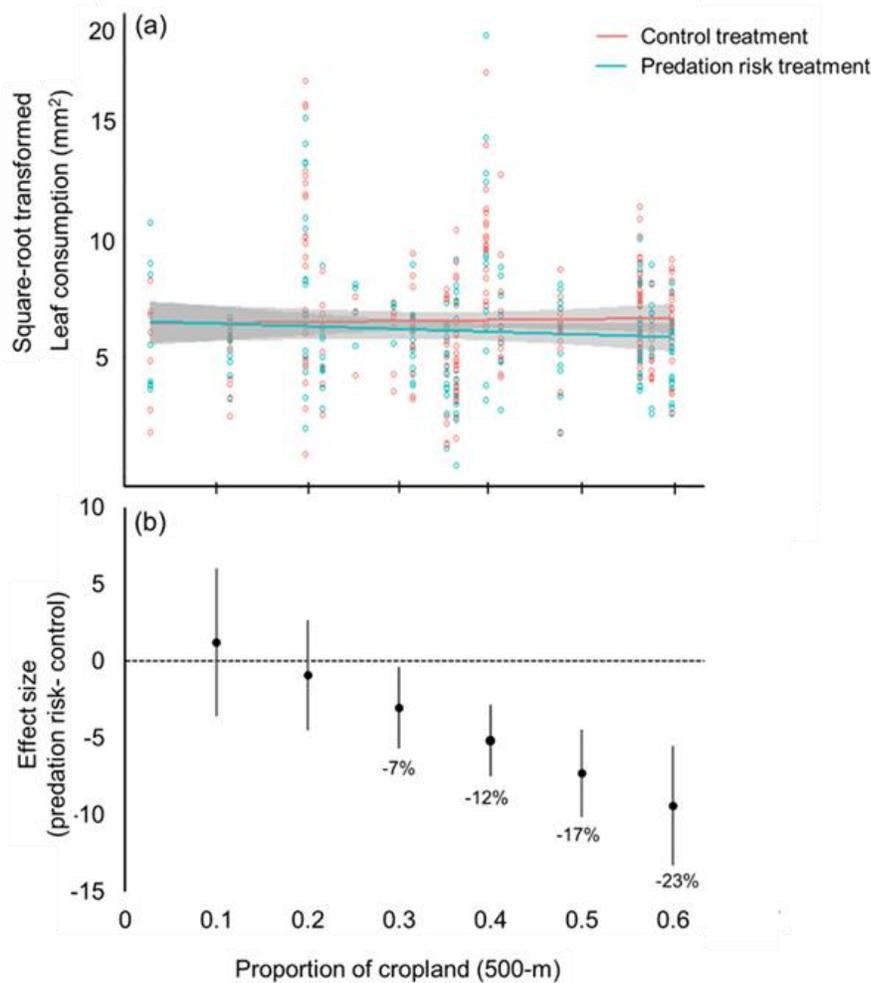


Fig. 4. Effect of exposure to predaceous stink bugs (*P. maculiventris*) on leaf consumption of CPB larvae derived from landscapes of varying complexity. In the top figure (a), each data point represents leaf consumption of a single larva. The bottom figure (b) is the effect size (mean \pm 95% CI) for larval leaf consumption based on the differences in the marginal means between predation risk and control treatments. A negative effect size indicates that larvae exposed to predators reduced leaf consumption relative to predator-free control. Percent differences between predation risk and control treatments are shown for significant effects ($P \leq 0.05$). Summary statistics of the mixed-effect model used to estimate marginal means and confidence intervals are available in Appendix S1.

DISCUSSION

The importance of landscape heterogeneity in driving variation in antipredator responses has been a cornerstone of much of the past research in predator–prey relationships (Laundré et al. 2001, Gaynor et al. 2019), but rarely in the context of agricultural systems. Consistent with prior laboratory work with CPB (Kaplan et al. 2014, Tigreros 2017), we found that the presence of non-lethal predators resulted in reduced larval foraging activity, and decreased leaf consumption by an average of 13%. The magnitude of prey responses (i.e., reduced feeding) was influenced by the abundance of predators in the fields where parents were collected. Predator abundance in turn varied across the landscape, peaking in crop-dominated landscapes (i.e., simple landscapes). This landscape-driven variation in predator abundance was associated with the spatial heterogeneity in the magnitude of antipredator responses. Indeed, predator-induced reductions in feeding were exacerbated in simple landscapes. We also report that CPB populations from high predation risk landscapes exhibited increased levels of intra-clutch cannibalism, a behavior known to decrease larval probability of being predated (Tigreros et al. 2017). These findings are broadly consistent with the ‘landscape of fear’ hypothesis (Laundré et al. 2014; Atuo and O’Connell 2017) which predicts that prey adaptively respond to spatial variation in predation risk. In other words, prey may adjust their behavioral responses to match the pattern of predation risk of its immediate environment, and in doing so, increase its survival. Although this phenomenon has been well documented in mammalian predator–prey interactions (Brown 1999, Laundré et al. 2001), this is the first study providing empirical evidence of the occurrence of a ‘landscape of fear’ in an herbivorous insect.

Prey can respond to the risk of predation in two major ways: disperse to predator-safe habitats or adjust behavior through phenotypic plasticity (Benard 2004, Chalfoun and Martin 2010). In the context of CPB larvae, dispersal abilities are limited. In fact, CPB larvae often remain on the natal plant even if it is completely defoliated (Collie et al. 2013). Thus, for CPB larvae, survival under predation threat will likely depend on the plasticity of traits that protect

them against predation. Consistent with this expectation, we found that prey collected from high predator-risk landscapes had stronger antipredator responses (i.e., decreases in leaf feeding and increases in intra-clutch cannibalism). Previous studies examining the relationship between predator abundance and predation rates on CPB eggs demonstrated that field predation is indeed higher when local fields contained more predators (Chang and Snyder 2004). It is therefore reasonable to assume that predation risk was proportional to the abundance of predators. By experimentally manipulating predation risk with “non-lethal predators” in the lab, we further validated the patterns observed in the field. That is, antipredator responses became progressively stronger as we moved from complex to simple landscapes where predators were more abundant. Our results thus provide clear evidence that landscape-level variation in predation risk led to behavioral adjustments among populations of an important agricultural insect pest.

Landscape heterogeneity not only mediated the magnitude of antipredator responses by influencing predator abundance, but also by affecting prey size at adulthood. Landscape composition affects body size across a wide range of invertebrate taxa (Gámez-Virués et al. 2015, Renauld et al. 2016, Oliveira et al. 2016), presumably through differences in the quality or quantity of resources available. Indeed, we found a significant correlation between the proportion of cropland in the landscape and the area devoted to cultivated solanaceous crops (i.e., the only suitable host for CPB) (Pearson’s $r = 0.80$, $P = 0.002$) which may explain, at least in part, the observed increase in body size in crop-dominated landscapes.

Irrespective of the causal mechanism driving body size variation, we found that maternal body size *per se* was inversely related to intra-clutch cannibalism. A recent study demonstrated that as predation risk increases, CPB females produced more trophic eggs as a means to promote intra-clutch cannibalism, and consequently improve the expression of antipredator responses (i.e., reduced feeding) (Tigreros et al. 2017). The number of trophic eggs, however, is also determined by several other factors, including maternal body size. In general, better-fed, larger mothers often produce egg masses consisting of more viable eggs of relatively large body size and fewer trophic eggs (Kudo and Nakahira 2004). Increased offspring size could confer an

advantage against predation, particularly in species like CPB where smaller individuals are more vulnerable to predation (Hilbeck and Kennedy 1996). Smaller females, by contrast, are unable to produce large eggs, but can actively increase offspring condition by producing more trophic eggs at the expense of producing fewer viable eggs (Kudo and Nakahira 2004). If these mechanisms hold true in our system, this might suggest that CPB may use different antipredator strategies depending on the phenotype of the mother; large females may rely more on increasing individual egg size, whereas small females may promote intra-clutch cannibalism by adjusting the number of trophic eggs produced. Some studies of offspring-size plasticity have provided experimental support of such adaptive maternal effects (Kudo and Nakahira 2005, Filippi et al. 2012, Hagmayer et al. 2018), but the underlying mechanisms operating in our system remains to be determined.

Our results are not in line with findings of both qualitative (Veres et al. 2013) and quantitative (Chaplin-Kramer et al. 2011) syntheses that found landscapes with large amounts of natural habitat support a more abundant community of natural enemies. Instead, ladybird beetles were more abundant in crop-dominated landscapes. Such effects are expected when the community of predators is dominated by agrobiont species that rely more on resources from agricultural fields (Tscharntke 2016). Work with *Coleomegilla maculata* and *Hippodamia convergens*—two of the most abundant species collected in our study—showed that these ladybird beetles may be more adapted to open habitats such as croplands than to enclosed/complex environments like forest (Gardiner et al. 2009, Werling et al. 2011). Moreover, aphids in potato fields could provide an abundant food source, allowing ladybird beetles to build up larger populations in crop-dominated landscapes than in complex landscapes. Previous field studies reported that ladybird beetles are drawn to potato fields by the presence of aphids, but once there they also feed extensively on CPB eggs and larvae (Snyder and Clevenger 2004).

Our work has implications for advancing our understanding of the range of mechanisms by which biological control could be strengthened in agricultural landscapes. Most landscape-

scale studies of biological control services have focused on assessing the influence of predator diversity or abundance on pest densities assuming they are a reasonable proxy for plant protection (Karp et al. 2018). Our results suggest that this perspective may underestimate the true biocontrol benefits provided by predators because the presence of predators in itself may potentially reduce pest feeding damage, even in the absence of actual predation. Similar results are increasingly documented in other pest-natural enemy associations (Steffan and Snyder 2010, Ninkovic et al. 2013, Thaler et al. 2014), and non-consumptive effects are now coming to the forefront of biocontrol research (Hermann and Landis 2017). The theoretical framework of using non-consumptive effects for managing pest population is sound, but its practical implementation under field conditions remains a challenge. To advance this line of inquiry, we use the findings observed in our study to suggest three directions where future studies will be particularly valuable to improve our understanding of non-consumptive effects in heterogeneous agricultural landscapes. First, while measuring changes in prey behavior can provide insights into mechanisms of risk effects, understanding whether risk effects have measurable effects on plant damage is arguably most relevant from a plant protection perspective. Second, landscape composition shaped antipredator responses through a shifting combination of resource and risk gradients, strongly suggesting that integrating both sources of variability could improve our ability to predict the magnitude of non-consumptive effects. For example, CPB females reproducing in simple landscapes experience conflicting effects of high predation risk and high crop-resource availability, which have opposing influences on offspring survival and phenotype. Previous laboratory research has documented such dynamic trade-offs in pest populations (Kaplan and Thaler 2010, Kaplan et al. 2014), but trials that span more realistic spatiotemporal scales are needed to improve the relevance of such experiments. Finally, the complex interplay between antipredator responses, and multiple biotic (e.g., predators and food quality) and abiotic stressors (e.g., land-use change and pesticides) make it difficult to predict the overall consequences of non-consumptive effects on pest control. This calls for the development of models to simulate pest population dynamics under variable land-use change scenarios.

REFERENCES

- Atuo, F.A., and O'Connell. T.J. 2017. The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. *Ecology and Evolution* 7: 4782-4793.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Softw.* 67: 1–48.
- Bell, A.M., Dingemanse, N.J., Hankison, S.J., Langenhof, M.B.W., and Rollins, K. 2011. Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks. *Journal of Evolutionary Biology* 24: 943–953.
- Benard, M.F. 2004. Predator-Induced Phenotypic Plasticity in Organisms with Complex Life Histories. *Annual Review of Ecology, Evolution, and Systematics* 35: 651-573.
- Brown, J.S., Laundré, J.W., and Gurung, M. 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy* 80: 385–399.
- Buchanan, A., Hermann, S., Lund, M., and Szendrei, Z. 2017. A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics. *Oikos* 126: 1233-1240.
- Burnham, K. P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Page Springer, New York, New York, USA.
- Chalfoun, A.D., and Martin, T.E. 2010. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a “win-stay, lose-switch” strategy? *Oecologia* 163: 885–892.
- Chang, G.C, and Snyder W.E. 2004. The relationship between predator density, community composition, and field predation of Colorado potato beetle eggs. *Biological Control* 31: 453–461.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., and Kremen, C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14: 922–

932.

- Collie, K., Kim, S.J., and Baker, M.B. 2013. Fitness consequences of sibling egg cannibalism by neonates of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Anim. Behav.* 85: 329–338.
- Filippi, L., Hironaka, M., and Nomakuchi, S. 2012. Individual Variation in Trophic Egg Production: Evidence for Maternal Manipulation in Response to Resource and Competition Levels. *ethology* 118: 503-510.
- Finke, D., and Snyder, W. 2010. Conserving the benefits of predator biodiversity. *Biological Conservation* 143: 2260–2269.
- Gómez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H.,... Westphal, C. 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications* 6: 8568.
- Gardiner, M.M., Landis, D.A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., Chacon, J. Heimpel, G.E., and DiFonzo, C.D. 2009. Landscape composition influences patterns of native and exotic lady beetle abundance. *Divers. Distrib.* 15: 554–564.
- Gaynor, K M., Brown, J.S., Middleton, A.D., Power, M.E., and Brashares, J.S. 2019. Landscapes of Fear: Spatial Patterns of Risk. *Trends in Ecology & Evolution*: 2486.
- Griffin, J.N., Byrnes J.E., and Cardinale B.J. 2013. Effects of predator richness on prey suppression: a meta-analysis. *Ecology* 94: 2180–2187.
- Hagmayer, A., Furness, A. I., Reznick, D. N., and Pollux, B. 2018. Maternal size and body condition predict the amount of post-fertilization maternal provisioning in matrotrophic fish. *Ecology and evolution* 8: 12386–12396.
- Hermann, S., and Landis, D. 2017. Scaling up our understanding of non-consumptive effects in insect systems. *Current Opinion in Insect Science* 14:54–60.
- Hermann, S. L., and Thaler, J. S. 2014. Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia* 176: 669–676.

- Hilbeck, A., and Kennedy G. 1996. Predators Feeding on the Colorado Potato Beetle in Insecticide-Free Plots and Insecticide-Treated Commercial Potato Fields in Eastern North Carolina *Biological Control* 6: 273–282
- Hillaert, J., Vandegehuchte, M.L., Hovestadt, T., and Bonte, D. 2018. Information use during movement regulates how fragmentation and loss of habitat affect body size. *Proc. R. Soc. B* 285.
- Hough-Goldstein J.A., Heimpel, G.E., Bechmann, H.E., and Mason, C.E. 1993. Review: Arthropod natural enemies of the Colorado potato beetle. *Crop Protection* 12: 324-334.
- Kaplan, I., McArt, S.H., and Thaler, J.S. 2014. Plant Defenses and Predation Risk Differentially Shape Patterns of Consumption, Growth, and Digestive Efficiency in a Guild of Leaf-Chewing Insects. *PLoS ONE* 9: e93714.
- Kaplan, I., Thaler, J.S. 2010. Plant resistance attenuates the consumptive and non-consumptive impacts of predators on prey. *Oikos* 119: 1105–1113.
- Karp, D.S. et al. 2018 Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences of the United States of America* 115: E7863–E7870.
- Kudo, S., and Nakahira, T. 2004. Effects of Trophic-Eggs on Offspring Performance and Rivalry in a Sub-Social Bug. *Oikos* 107: 28-35.
- Kudo, S., and Nakahira, T. 2005: Trophic-egg production in a subsocial bug: adaptive plasticity in response to resource conditions. *Oikos* 111, 459—464.
- Laundré, J.W., Hernández, L. and Altendorf, K.B. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79: 1401–1409.
- Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., ... Browning, D. M. 2014. The landscape of fear: The missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95: 1141–1152.
- Lefcheck, J. S. 2016. *piecewiseSEM: Piecewise structural equation modeling in R for ecology,*

- evolution, and systematics. *Methods in Ecology and Evolution* 7: 573-579.
- Lenth, R., Singmann, H., Love, J., and Buerkner, P. H. M. 2018. emmeans: Estimated Marginal Means, aka LeastSquares Means. R Packag. version 1.2.3.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48: 25–34.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- McClure, M., and Despland, E. 2011. Defensive responses by a social caterpillar are tailored to different predators and change with larval instar and group size. *Naturwissenschaften* 98: 425–43.
- Ninkovic, V., Feng, Y., Olsson, U., and Pettersson, J. 2013. Ladybird footprints induce aphid avoidance behavior. *Biol. Control* 65: 63-71.
- Oliveira, M. O., Freitas, B. M., Scheper, J. and Kleijn, D. 2016. Size and Sex-Dependent Shrinkage of Dutch Bees during One-and-a-Half Centuries of Land-Use Change. *PLoS One* 11, e0148983.
- Pfannenstiel, R.S., Hunt, R.E., and Yeargan, K.V. 1995. Orientation of a Hemipteran predator to vibrations produced by feeding caterpillars. *J. Insect Behav.* 8: 1–9.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Development Core Team, R. 2015. nlme: linear and nonlinear mixed effects models. R Packag. version 3.1-122 R package, 1–3.
- Preisser, E., Bolnick, D., and Benard, M. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86: 501-509.
- Preisser E.L., and Orrock J.L. 2012. The allometry of fear: interspecific relationships between body size and response to predation risk. *Ecosphere* 3: 1-27.
- Renauld, M., Hutchinson, A., Loeb, G., Poveda, K. and Connelly, H. 2016. Landscape simplification constrains adult size in a native ground-nesting bee. *PLoS ONE* 11:e0150946
- Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field

- interaction webs. *American Naturalist* 151: 327–342.
- Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90:363–368.
- Snyder W.E., and Clevenger, G.M. 2004. Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles. *Biological Control* 31: 353–361.
- Stefan, S.A., and Snyder, W.E. 2010. Cascading diversity effects transmitted exclusively by behavioral interactions. *Ecology* 91: 2242-2252.
- Thaler, J. S., McArt, S.H. and Kaplan, I. 2012. Compensatory mechanisms for ameliorating the fundamental tradeoff between predator avoidance and foraging. *Proceedings of the National Academy of Sciences of the United States of America* 109: 12075–12080.
- Thaler, J.S., Contreras, H., and Davidowitz, G. 2014. Effects of predation risk and plant resistance on *Manduca sexta* caterpillar feeding behaviour and physiology. *Ecol. Entomol.* 39: 210-216.
- Tigeros, N., Norris, R. H., Wang, E. H., and Thaler, J. 2017. Maternally induced intraclutch cannibalism: An adaptive response to predation risk?. *Ecology Letters* 20: 487–494
- Tigeros, N., Wang, E., and Thaler, J. 2018. Prey nutritional state drives divergent behavioural and physiological responses to predation risk. *Functional Ecology* 32: 982-989.
- 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. 2017. New York cropland data layer (2014-15 ed.). 684 USDA-NASS, Washington, D.C, USA. <https://nassgeodata.gmu.edu/CropScape/>
- Veres, A., Petit, S., Conord, C., and Lavigne, C. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agric Ecosyst Environ* 160:110–117.
- Weisz, R., Smilowitz, Z., Fleischer, S. 1996. Evaluating risk of Colorado potato beetle (Coleoptera: Chrysomelidae) infestation as a function of migratory distance. *J Econ Entomol.* 89: 435–441.

Werling, B.P., Meehan, T.D., Gratton, C., and Landis, D.A. 2011. Influence of habitat and landscape perennality on insect natural enemies in three candidate biofuel crops.

Biol.Control 59: 304–312.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag New York.

APPENDIX S1

Supplementary Material Chapter 1: Contrasting effects of landscape composition on crop yield mediated by specialist herbivores.

This supporting information includes the following:

Table S1.1. Landscape composition and habitat diversity at 250, 500 and 1000 m.

Table S1.2. Matrix of the correlation coefficients among landscape variables included in the models.

Table S1.3. Model selection for landscape effects on lepidoptera incidence, aphid incidence and flea beetle abundance.

Table S1.4. Model selection for Parasitoid-host ratios.

Table S1.5. Model selection for landscape effects on plant damage and crop yield.

Table S1.6. Test of conditional independence claims associated with the path model shown in FIG. 6.

Table S1.1. Proportion of meadows, seminatural habitats, cropland, and landscape diversity (Shannon- Wiener index) at 250, 500 and 1000 m around the experimental fields.

Scale	Meadows		Seminatural habitats		Cropland		Landscape diversity index	
	min	max	min	max	min	max	min	max
250	3.5	71.5	0	64.7	0	90.0	1.26	2.61
500	0.3	67.0	1.0	76.4	0.7	80.7	1.55	2.72
1000	7.0	53.8	5.8	86.9	1.7	62	1.90	2.67

Table S1.2. Matrix of the correlation coefficients among landscape variables included in the models. Bold font indicates significant correlations (Pearson correlation $p < 0.05$).

Landscape variable/scale	Cropland/250	Cropland/500	Cropland/1000	Meadows/250	Meadows/500	Meadows/1000	Seminatural habitats/250	Seminatural habitats/500
Cropland/ 250								
Cropland/ 500	0.8943							
Cropland/1000	0.6584	0.6758						
Meadows/250	-0.3317	-0.2763	0.1138					
Meadows/ 500	-0.2167	-0.2393	0.2224	0.8813				
Meadows/1000	0.1384	0.0513	0.2491	0.6153	0.7096			
Seminatural habitats/250	-0.4487	-0.3994	-0.2487	-0.0068	0.0197	-0.1592		
Seminatural habitats/500	-0.2448	-0.3396	-0.2347	-0.0272	-0.0889	-0.1078	0.8574	
Seminatural habitats/1000	-0.1505	-0.1072	-0.3571	-0.1703	-0.2528	-0.3763	0.7179	0.7801

Table S1.3. Model selection for landscape effects on lepidoptera incidence, aphid incidence and flea beetle abundance. The overall best model (most parsimonious), competing models ($AICc \leq 2$) and the average models are presented. The overall best models are bolded. The number of parameters in the model (k), the AICc, AICc difference ($\Delta AICc$) and determination coefficients (R^2) are given for each model. Values in parentheses correspond to the contribution (i.e., importance) of each variable calculated over the best set of models. Models were selected using the dredge function based on second order Akaike Information Criterion (AICc). Mean and significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$) are given for the coefficients of each linear mixed effects model.

Response variable	Model	AICc	$\Delta AICc$	R ²	k	Landscape variables						Year				
						Cropland			Semi-natural areas				Meadows			
						250 m	500 m	1000 m	250 m	500 m	1000 m		250 m	500 m	1000 m	
Lepidoptera incidence	1	-32.7	0.00	0.718	2									-0.454***	+***	
	2	-32.3	0.34	0.764	3		-0.211							-0.521***	+***	
	3	-31.6	1.10	0.749	3	-0.141								-0.485***	+***	
	4	-31.2	1.48	0.725	3			-0.212						-0.440***	+***	
	Average model	-30.9	1.80	0.755	5	-0.141 (0.20)	-0.062 (0.29)	-0.035 (0.16)						-0.477 (1)	0.268 (1)	
Aphids incidence	1	-15.1	0.00	0.575	2								0.658*		+***	
	2	-14.5	0.62	0.635	3								0.483*	0.456	+***	
	3	-13.8	1.38	0.587	2							0.723			+***	
	4	-13.3	1.84	0.609	3				-0.206	0.623*						+***
	Average model	-13.4	1.7	0.642	5				-0.020 (0.15)	0.498 (0.81)	0.088 (0.19)	0.121 (0.28)				0.319 (1)
Flea beetles abundance	1	117.4	0.00	0.447	3					2.235			2.61**		+*	
	2	117.7	0.28	0.482	3					2.356			2.902**		+*	
	3	119.2	1.79	0.464	2								2.235**		+*	
	Average model	116.3	1.1	0.466	4					1.882 (0.82)			1.547 (0.62)	1.108 (0.38)		-0.745 (1)

Table S1.4. Model selection for landscape effects on Parasitoid-host ratios. The overall best model (most parsimonious), competing models ($AICc \leq 2$) and the average models are presented. The overall best models are in bold type. The number of parameters in the model (k), the AICc, AICc difference ($\Delta AICc$) and determination coefficients (R^2) are given for each model. Values in parentheses correspond to the contribution (i.e., importance) of each variable calculated over the best set of models. Models were selected using the dredge function based on second order Akaike Information Criterion (AICc). Mean and significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$) are given for the coefficients of each linear mixed effects model.

Response variable	Model	AICc	$\Delta AICc$	R2	k	Landscape variables								
						Cropland			Semi-natural areas			Meadows		
						250 m	500 m	1000 m	250 m	500 m	1000 m	250 m	500 m	1000 m
	1	-14.5	0.00	0.843	1						-			
	2	-13.0	1.50	0.627	1						0.682			0.844*
Parasitoid-host ratio	Average model	-14.2	0.30	0.769	2						-			
											0.439		0.300	
											(0.59)		(0.41)	

Table S1.6. Test of conditional independence claims associated with the path model shown in FIG.6.

D-sep claim of independence	Mix effect model*	<i>p</i> value
$(X_4; X_6) \{X_3, X_8\}$	$X_6 \sim \mathbf{X_4} + X_3 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.547
$(X_4; X_1) \{X_2\}$	$X_1 \sim \mathbf{X_4} + X_2, \text{ random} = \sim 1 \text{study areas/field}$	0.529
$(X_3; X_5) \{X_4, X_8\}$	$X_5 \sim \mathbf{X_3} + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.894
$(X_3; X_7) \{X_4, X_8\}$	$X_7 \sim \mathbf{X_3} + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.138
$(X_3; X_1) \{X_2\}$	$X_1 \sim \mathbf{X_3} + X_2, \text{ random} = \sim 1 \text{study areas/field}$	0.614
$(X_8; X_1) \{X_2\}$	$X_1 \sim \mathbf{X_8} + X_2, \text{ random} = \sim 1 \text{study areas/field}$	0.403
$(X_5; X_6) \{X_4, X_8\}$	$X_6 \sim \mathbf{X_5} + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.514
$(X_5; X_7) \{X_4, X_8\}$	$X_7 \sim \mathbf{X_5} + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.206
$(X_5; X_1) \{X_2, X_4, X_8\}$	$X_1 \sim \mathbf{X_5} + X_2 + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.131
$(X_6; X_7) \{X_3, X_4, X_8\}$	$X_7 \sim \mathbf{X_6} + X_3 + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.392
$(X_6; X_1) \{X_2, X_3, X_8\}$	$X_1 \sim \mathbf{X_6} + X_2 + X_3 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.877
$(X_7; X_2) \{X_3, X_4, X_5, X_6, X_8\}$	$X_2 \sim \mathbf{X_7} + X_3 + X_4 + X_5 + X_6 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.957
$(X_7; X_1) \{X_2, X_4, X_8\}$	$X_1 \sim \mathbf{X_7} + X_2 + X_4 + X_8, \text{ random} = \sim 1 \text{study areas/field}$	0.926

Notes: The notation ‘ $(X, Y) | \{A, B, \dots\}$ ’ means that variables X and Y are d-separated, and hypothesized to be probabilistically independent, conditional on the set of variables $\{A, B, \dots\}$ (Shiplely 2004).

X_1 = crop yield (square root transformed), X_2 = plant damage (log-transformed), X_3 = proportion of meadows in a 1000m radius, X_4 = proportion of meadows in a 250 m radius, X_5 = flea beetle abundance (log-transformed), X_6 = Lepidoptera incidence (square root transformed), X_7 = aphid incidence (square root transformed), X_8 = Year of study.

Each independent claim was tested using mixed effect models obtained in R with the nlme package. The factors in bold are those dependent variables whose partial regression slope should be not significantly different from zero ($p > 0.05$) if the pair of variables (X, Y) are statistically independent.

REFERENCES

Shipley, B. 2004. Analyzing the allometry of multiple interacting traits. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 235-241.

APPENDIX S2

Supplementary Material Chapter 2: Effectiveness of augmentative biological control depends on landscape context.

This supporting information includes the following:

Supplementary Table S2.1. Model selection for effects of landscape composition and potential interactions with predator releases on lepidopteran larval abundance, plant damage, crop biomass, predation rates, and natural enemy abundance.

Supplementary Table S2.2. Results of Mantel test of spatial autocorrelation in the residuals of the final models.

Supplementary Table S2.3. Statistical models for the effects of landscape composition and potential interactions with predator releases on both final crop yield quality and crop yield quantity.

Supplementary Fig. S2.1. The effect of augmentative releases of predators on final crop yield based on quality and quantity measures in landscapes of varying complexity.

Supplementary Table S2.1. Model selection for landscape effects and potential interactions with predator releases on lepidopteran larval abundance, plant damage, crop biomass, predation rates, and natural enemy abundance. The overall best model (most parsimonious) and competing models are presented. The overall best models are bolded. The AICc values, AICc difference (Δ AICc) and conditional coefficient of determination¹ (R^2) are given for each model. Models were selected based on second order Akaike Information Criterion (AICc).

Response variable	Landscape variable	Scale (m)	Model	AICc	Δ AICc	R^2
Lepidoptera abundance	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	53.645	3.322	0.733
	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	50.322	0	0.766
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	51.818	1.496	0.760
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	55.563	5.241	0.795
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	58.143	7.820	0.760
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	59.684	9.361	0.730
Plant damage	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	257.881	7.465	0.638
	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	256.400	5.984	0.690
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	250.417	0	0.738
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	274.720	24.303	0.656
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	274.635	24.218	0.627
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	272.128	21.711	0.637
Crop biomass	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	341.324	1.885	0.923
	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	345.487	6.048	0.916
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	339.440	0	0.926
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	346.151	6.712	0.915
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	346.367	6.928	0.915
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	343.703	4.263	0.913
Predation on sentinel larvae	Cropland	500	Intercept + Cropland + Treatment	310.208	1.749	0.523
	Cropland	1000	Intercept + Cropland + Treatment	310.163	1.703	0.523
	Cropland	2000	Intercept + Cropland + Treatment	309.700	1.240	0.523
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment	309.793	1.333	0.517
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment	308.594	0.134	0.525
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment	308.460	0	0.519
	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	228.673	2.966	0.528

Predation on sentinel eggs	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	227.791	2.084	0.528
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	226.908	1.202	0.554
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	227.561	1.854	0.570
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	227.748	2.041	0.543
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	225.707	0	0.584
Ground-dwelling predators	Cropland	500	Intercept + Cropland + Treatment	271.105	3.133	0.720
	Cropland	1000	Intercept + Cropland + Treatment	270.958	2.987	0.701
	Cropland	2000	Intercept + Cropland + Treatment	267.972	0	0.743
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment	273.531	5.559	0.723
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment	273.324	5.352	0.717
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment	271.174	3.203	0.737
Parasitoids	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	34.934	6.786	0.920
	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	30.626	2.478	0.924
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	31.580	3.431	0.914
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	33.199	5.050	0.927
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	28.149	0	0.937
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	32.521	4.373	0.921
Foliar-foraging predators	Cropland	500	Intercept + Cropland + Treatment + Cropland *Treatment	437.467	2.332	0.581
	Cropland	1000	Intercept + Cropland + Treatment + Cropland *Treatment	438.696	3.561	0.576
	Cropland	2000	Intercept + Cropland + Treatment + Cropland *Treatment	438.556	3.422	0.576
	Semi-natural areas	500	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	435.135	0	0.620
	Semi-natural areas	1000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	436.075	0.941	0.615
	Semi-natural areas	2000	Intercept + Semi-natural+ Treatment + Semi-natural*Treatment	435.922	0.787	0.607

1. The conditional R^2 values for each model (variance explained by both the fixed and random factors) were calculated using the methods detailed in Nakagawa and Schielzeth (2013).

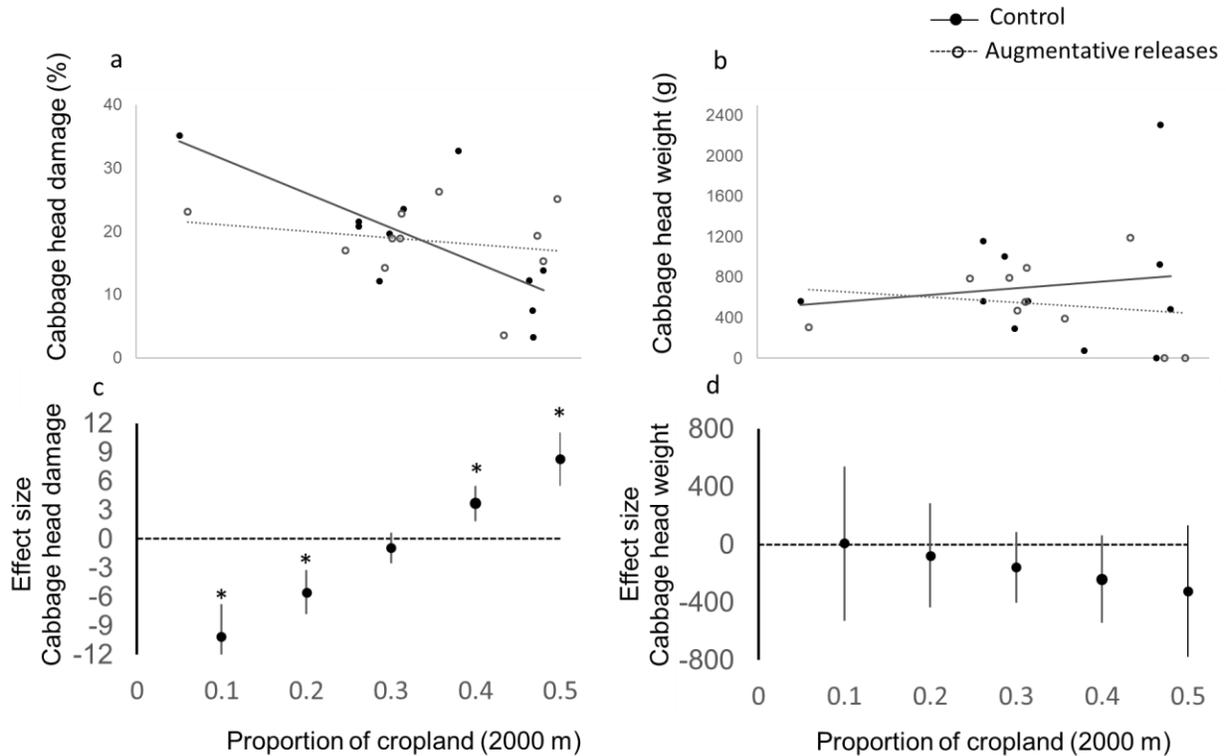
Supplementary Table S2.2. Results of Mantel test¹ of spatial autocorrelation in the residuals of the final models. All response variables have p-values > 0.05 indicating no pattern of similarity due to spatial proximity.

Response variable / landscape variable	Monte-Carlo test Observation	P-value
Lepidoptera abundance / Cropland 1000 m	-0.021	0.782
Plant Damage / Cropland 2000 m	-0.061	0.999
Crop biomass / Cropland 2000 m	-0.023	0.797
Predation on sentinel larvae/ Semi-natural areas 2000 m	0.002	0.415
Predation on sentinel eggs/ Semi-natural areas 2000 m	-0.026	0.805
Ground-dwelling predators / Cropland 1000 m	-0.028	0.818
Parasitoids / Semi-natural areas 1000 m	-0.015	0.624
Foliar-foraging predators/ Semi-natural areas 500 m	-0.003	0.477

1. All final models were tested for spatial autocorrelation in the residuals using the mantel test from the package ade4 (Dray & Dufour 2007).

Effects of augmentative predator releases on final crop yield

For the purposes of this paper, we draw distinction between marketable crop yield and crop biomass. Marketable crop yield of cabbage is a result of both the harvested head weight and the cosmetic injury to the head. Crop biomass, on the other hand, is an indicator of plant productivity, which is significantly correlated with head weight (Pearson's $r = 0.58$, $P = 0.005$), but does not account for the quality component. In fact, although high levels of lepidopteran defoliation consistently increase feeding injury of cabbage plants (i.e., plant damage was significantly correlated with the mean abundance of lepidopteran larvae, Pearson's $r = 0.33$, $P = 0.002$), they may not always affect harvested head weight due to the ability of brassica crops to tolerate relatively high levels of defoliation without significantly affecting final weight (Burkness *et al.* 2005, Liu *et al.*, 2004). For this reason, we evaluated the potential effects of augmentative biocontrol on final crop yield using both quantity (i.e., marketable cabbage head weight) and quality (i.e., cabbage head damage) measures (Supplementary Fig. S2.1).



Supplementary Fig. S2.1. The effect of augmentative releases of predators on final crop yield based on (a) quality (i.e., cabbage head damage) and (b) quantity measures (i.e., cabbage head weight) in landscapes of varying complexity. Predicted responses for the control (solid lines) and augmentative release (dashed lines) treatments are calculated from the set of best supported linear mixed-effects models (lme4). Effects of the interactions between treatment and landscape complexity were significant ($P < 0.05$) for crop yield quality, but not for crop yield quantity. In the top Figures (a and b) every point represents the mean treatment value in a given experimental plot. The bottom figs. (c and d) are effect sizes (mean \pm 95 % CI) for crop yield quality (c) and crop yield quantity (d) based on the difference in the marginal means between plots with and without predator releases across the landscape complexity gradient. A positive effect size indicates that the mean of the predator plots is larger than the mean of control plots, while a negative effect size indicates a higher control mean. Pairwise comparisons were individually calculated at even intervals across the landscape complexity gradient. Asterisks denote effect sizes that are significantly different from zero ($P < 0.05$). Summary statistics of the LMER models used to estimate marginal means and confidence intervals are available in Supplementary Table S3.

Supplementary Table S2.3. Statistical models for the effects of landscape composition and potential interactions with predator releases on both final crop yield quality (i.e., cabbage head damage) and quantity (i.e., cabbage head weight). Statistical models were used to estimate mean and 95% CI of effect sizes for landscape effects and potential interactions with predator releases (Supplementary Fig. S1.). Dashed lines represent interaction terms not included in the final models because they were not significant ($P > 0.05$). Boldface text indicates significant relationships ($P < 0.05$).

Response variables and predictors	d.f.¹	F¹	P-value¹
Crop yield quality (i.e., cabbage head damage)			
Cropland (2000 m)	1, 29.898	2.823	0.103
Treatment (control and predator releases)	1, 32.556	16.287	< 0.001
Interaction (cropland x treatment)	1, 32.517	18.995	< 0.001
Crop yield quantity (i.e., cabbage head weight)			
Cropland (2000 m)	1, 2182.4	0.233	0.629
Treatment (control and predator releases)	1, 3137.8	1.196	0.274
Interaction (cropland x treatment)	-----	-----	-----

1. The statistical significance of fixed effects and interaction terms were estimated using mixed-effect models (lmer) interpreted with a Satterthwaite approximation (Kuznetsova *et al.* 2017, Luke 2017).

REFERENCES

- Burkness E., Gingera G.J. & Hutchison W. D. 2005. Impact of simulated insect defoliation and timing of injury on cabbage yield in Minnesota. *Great Lakes Entomologist* **38**, 1-12 (2005).
- Dray, S. & Dufour. A. B. The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.* **22**, 1–20 (2007).
- Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest Package: Tests in Linear Mixed Effects Models. *J. Stat. Softw.* **82**, (2017).
- Liu S.-S. Shi Z.-H. Guo S.-J. Chen Y.-N. Zhang G.-M. Lu L.-F. Wang D.-S. Deuter P. Zalucki M. P. Improvement of crucifer IPM in the Changjiang River Valley, China: from research to practice, pp. 61–66. In Endersby N. M. Ridlands P. M. [eds.], *The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the 4th International Workshop, 26–29 November 2001, Melbourne, Australia*. The Regional Institute, Gosford, Australia (2004).
- Luke, S. G. Evaluating significance in linear mixed-effects models in R. *Behav. Res. Methods* **49**, 1494–1502 (2017).
- Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, **4**, 133–142 (2013).

APPENDIX S3

Supplementary Material Chapter 3: Landscape composition mediates the relationship between predator body size and pest control

This supporting information includes the following:

1. **Supplementary Methods S3.1:** Video surveillance of predator activity on sentinel prey.
2. **Supplementary Methods S3.2:** Cluster analysis to separate ground beetle species based on body size.
3. **Table S3.1.** Model selection for landscape effects on skewness coefficients of body size distribution, community weighted variance of body size (CWV), and community weighted mean body size (CWM).
4. **Table S3.2.** Results of Mantel test of spatial autocorrelation in the residuals of the final models.
5. **Table S3.3.** Ecological information for the ground beetle species collected in this study, including species name, mean body size, body size category, and functional group.
6. **Table S3.4.** Statistical models for the effects of different components of ground beetle community structure and potential interactions with the proportion of cropland at the 1000 m spatial scale on predation rates on sentinel diamondback moth pupae.
7. **Fig. S3.1.** Setup of the video surveillance system used to monitor predation events on sentinel prey.
8. **Fig. S3.2.** Average proportion of predator visits by different morphotaxa on sentinel prey.
9. **Fig. S3.3.** Relationship between the proportion of the total predator visits to sentinel prey made by carabid beetles and the proportion of cropland in a 1000 m radius.
10. **Fig. S3.4.** Dendrogram of the agglomerative hierarchical clustering analysis separating clusters of ground beetle species based on body size.
11. **Fig. S3.5.** Relationships between ground beetle species richness (i.e. number of species) and the proportion of cropland in a 1000 m radius.
12. **Fig. S3.6.** Relationship between predation rates on sentinel diamondback moth pupae and different components of ground beetle community structure.

Table S3.1. Model selection for landscape effects on skewness coefficients of body size distribution, community weighted variance of body size (CWV), and community weighted mean body size (CMW). The overall best model (most parsimonious) and competing models are presented. The overall best models are bolded. The AICc values, AICc difference (ΔAIC_c) and conditional coefficient of determination¹ (R^2) are given for each model. Models were selected based on second order Akaike Information Criterion (AICc).

Response variable	Landscape variable	Scale (m)	Model	AICc	ΔAIC_c	R^2
Skewness	Cropland	500	Intercept + Cropland	76.112	3.500	0.623
	Cropland	1000	Intercept + Cropland	72.612	0	0.653
	Cropland	2000	Intercept + Cropland	75.547	2.935	0.658
	Semi-natural areas	500	Intercept + Semi-natural	80.504	7.892	0.647
	Semi-natural areas	1000	Intercept + Semi-natural	79.397	6.785	0.659
	Semi-natural areas	2000	Intercept + Semi-natural	80.939	8.327	0.644
CWV	Cropland	500	Intercept + Cropland	224.001	1.009	0.403
	Cropland	1000	Intercept + Cropland	222.892	0	0.424
	Cropland	2000	Intercept + Cropland	224.348	1.456	0.412
	Semi-natural areas	500	Intercept + Semi-natural	223.845	0.953	0.458
	Semi-natural areas	1000	Intercept + Semi-natural	223.113	0.221	0.452
	Semi-natural areas	2000	Intercept + Semi-natural	224.262	1.370	0.447
CMW	Cropland	500	Intercept + Cropland	162.303	0.620	0.532
	Cropland	1000	Intercept + Cropland	161.683	0	0.506
	Cropland	2000	Intercept + Cropland	161.834	0.151	0.563
	Semi-natural areas	500	Intercept + Semi-natural	166.266	4.583	0.462
	Semi-natural areas	1000	Intercept + Semi-natural	164.746	3.063	0.491
	Semi-natural areas	2000	Intercept + Semi-natural	166.828	5.145	0.469

1. The conditional R^2 values for each model (variance explained by both the fixed and random factors) were calculated using the methods detailed in Nakagawa and Schielzeth (2013).

Table S3.2. Results of Mantel test¹ of spatial autocorrelation in the residuals of the final models (See Fig. 2 and Fig. S5). All response variables have p-values > 0.05 indicating no pattern of similarity due to spatial proximity.

Response variable / landscape variable	Monte-Carlo test Observation	P-value
Skewness of body size / Cropland 1000 m	0.006	0.393
Community weighted variance (CWV) / Cropland 1000 m	0.036	0.184
Community weighted mean (CWM) / Cropland 1000 m	-0.016	0.616
Species Richness / Cropland 1000 m	-0.041	0.832

2. All final models were tested for spatial autocorrelation in the residuals using the Mantel test from the package ade4 (Dray and Dufour 2007).

Table S3.3 (first part). Ecological information for the ground beetle species collected in this study, including species name, mean body size, body size category, and functional group.

Species	Mean Body size¹ (mm)	Body size category²	Functional group³
<i>Acupalpus pauperculus</i>	2.30	Small	Omnivorous
<i>Agonum cupripenne</i>	5.60	Small	Carnivorous
<i>Agonum muelleri</i>	5.10	Small	Carnivorous
<i>Agonum octopunctatum</i>	5.04	Small	Carnivorous
<i>Agonum placidum</i>	5.57	Small	Carnivorous
<i>Amara cupreolata</i>	4.80	Small	Herbivore
<i>Amara familiaris</i>	4.21	Small	Herbivore
<i>Anisodactylus sanctaecrucis</i>	6.21	Small	Omnivorous
<i>Bembidion affine</i>	1.95	Small	Carnivorous
<i>Bembidion quadrimaculatum</i>	2.14	Small	Carnivorous
<i>Bembidion rapidum</i>	2.70	Small	Carnivorous
<i>Bembidion versicolor</i>	1.82	Small	Carnivorous
<i>Brachinus ovipennis</i>	5.95	Small	Carnivorous
<i>Brachinus</i> sp.	6.22	Small	Carnivorous
<i>Bradycellus lecontei</i>	2.63	Small	Carnivorous
<i>Chlaenius sericeus</i>	9.69	Large	Carnivorous
<i>Chlaenius nemoralis</i>	7.95	Large	Carnivorous
<i>Chlaenius tricolor</i>	8.64	Large	Carnivorous
<i>Cicindela punctulata</i>	7.59	Large	Carnivorous
<i>Clivina bipustulata</i>	4.36	Small	Omnivorous
<i>Clivina fossor</i>	3.64	Small	Omnivorous
<i>Clivina</i> sp.	1.61	Small	Omnivorous
<i>Colliuris pensylvanica</i>	3.35	Small	Carnivorous
<i>Dyschirius erythrocerus</i>	2.28	Small	Carnivorous
<i>Dyschirius globulosus</i>	1.54	Small	Carnivorous
<i>Elaphropus anceps</i>	1.59	Small	Carnivorous

Table S3.3 (second part).

Species	Mean Body size¹ (mm)	Body size category²	Functional group³
<i>Harpalus affinis</i>	6.16	Small	Herbivore
<i>Harpalus caliginosus</i>	13.69	Large	Herbivore
<i>Harpalus erraticus</i>	9.39	Large	Herbivore
<i>Harpalus pennsylvanicus</i>	9.61	Large	Herbivore
<i>Harpalus compar</i>	6.02	Small	Herbivore
<i>Harpalus puncticeps</i>	9.64	Large	Herbivore
<i>Harpalus rufipes</i>	8.74	Large	Herbivore
<i>Loricera pilicornis</i>	5.22	Small	Carnivorous
<i>Paraclivina bipustulata</i>	4.38	Small	Carnivorous
<i>Patrobus longicornis</i>	7.86	Large	Carnivorous
<i>Platynus hypolithos</i>	8.74	Large	Carnivorous
<i>Poecilus chalcites</i>	7.32	Large	Carnivorous
<i>Poecilus lucublandus</i>	7.44	Large	Carnivorous
<i>Pterostichus melanarius</i>	10.44	Large	Carnivorous
<i>Pterostichus permundus</i>	8.71	Large	Carnivorous
<i>Pterostichus luctuosus</i>	10.57	Large	Carnivorous
<i>Pterostichus stygicus</i>	9.12	Large	Carnivorous
<i>Scarites subterraneus</i>	10.09	Large	Carnivorous
<i>Stenolophus comma</i>	4.42	Small	Omnivorous
<i>Stenolophus ochropezus</i>	4.37	Small	Omnivorous
<i>Stenolophus</i> sp.	3.88	Small	Omnivorous

1. Elytra length (i.e. the longest distance from the elytron apex to the elytron base) was digitally measured for all collected species. See main text for explanation.
2. Species were divided into two discrete size categories based on a cluster analysis. See Supplementary Methods S2 for explanation.
3. Species were classified into three diet categories according to their predominant feeding habits during the adult stage based on Bousquet (2010) and Homburg et al. (2013).

Supplementary Methods S3.1: Video surveillance of predator activity on sentinel prey

To quantify the relative contribution of carabid beetles to the overall predation rates along the landscape gradient, the sentinel prey experiment was accompanied by video surveillance of predation events using digital cameras (BirdCam® Pro - WCB-00116, Wingscapes, Calera, AL, USA) with a resolution of 2592 x 1944 pixels per square inch. Cameras are equipped with a night vision function, which allowed to record video footage for the entire 24 h that the sentinel prey were in the field. Cameras were attached to a metal fence post and positioned at ~0.30–0.5 m above the surface of the ground to secure precise placement and aiming (Fig. S1a). Each camera was protected from rain and direct sunlight by a plastic board (Coroplast®, Vanceburg, KY, USA) held approximately 15 cm above the camera (Fig. S1b). At each experimental plot, one of the 10 sentinel prey arenas was selected randomly and a camera was programmed to monitor sentinel prey over a 24 h period (Fig. S1c). Video surveillance of sentinel prey was conducted three times per plot each year at 15, 30, and 45 days after transplanting.



Fig. S3.1. Setup of the video surveillance system used to monitor predation events on sentinel prey (a-b). Photography captured with the video system showing a ground beetle approaching a sentinel prey (c-d).

Video recordings were reviewed following the methods of Grieshop et al. (2012). Briefly, all predators interacting with the sentinel prey were assigned to one of eight morphotaxa: Carabidae, Coleoptera (other than Carabidae), Formicidae, Gryllidae, Chilopoda, Opiliones, Araneae, and vertebrates. A predation event (i.e. predation visitation) was defined as an incidence in which a potential predator came within one centimeter of a sentinel prey (Grieshop et al. 2012) (Fig. S1d). Video data was analyzed in two-steps. First, data from all sampling dates and locations were pooled to calculate the average proportion of the total visits made by each predatory morphotaxa on sentinel prey (Fig. S2). In a second step, we evaluated the effect of landscape simplification on the proportion of predation visits by carabid beetles using a linear (nlme) mixed-effect model and conditional F-test (Pinheiro and Bates 2000; Fig. S3). The proportion of cropland at 1000 m radius was included as a fixed factor in the model, whereas “farm identity” and “year” were used as random factors to account for any environmental differences across sites and years. Model residuals were tested for normality and homoscedasticity assumptions following Zuur et al. (2009).

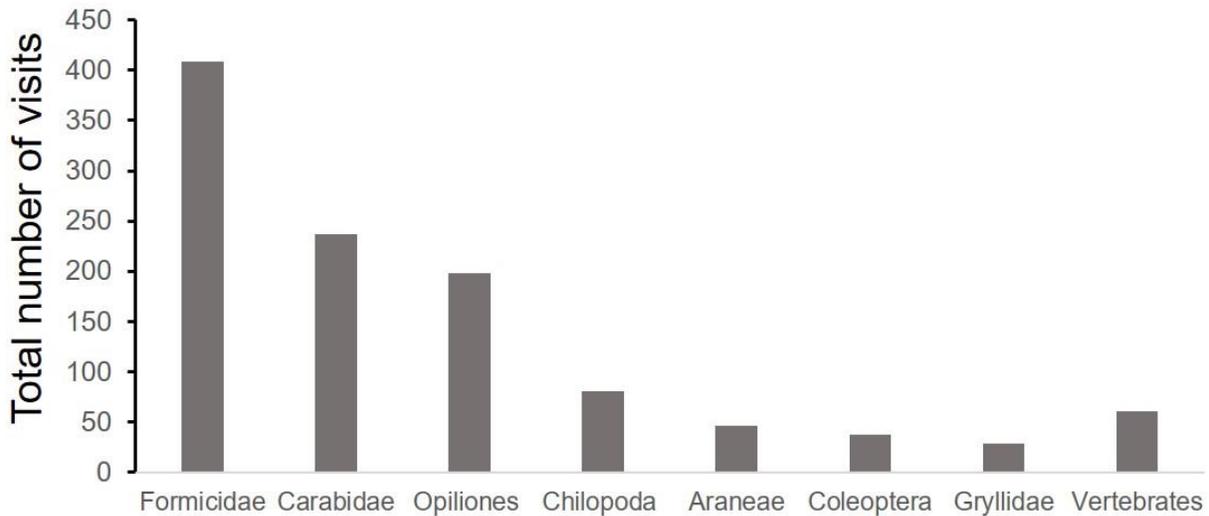


Fig. S3.2. Average proportion of predator visits by different morphotaxa on sentinel prey. Ants (37%), carabid beetles (22%), and opiliones (18%) were the dominant predators visiting sentinel prey over the course of the study. Other predatory taxa observed visiting sentinel prey included Chilopoda, Araneae, Coleoptera (i.e. Coccinellidae and Staphylinidae), Gryllidae, and small vertebrates (i.e. birds and rodents) that collectively accounted for 23% of the total visits.

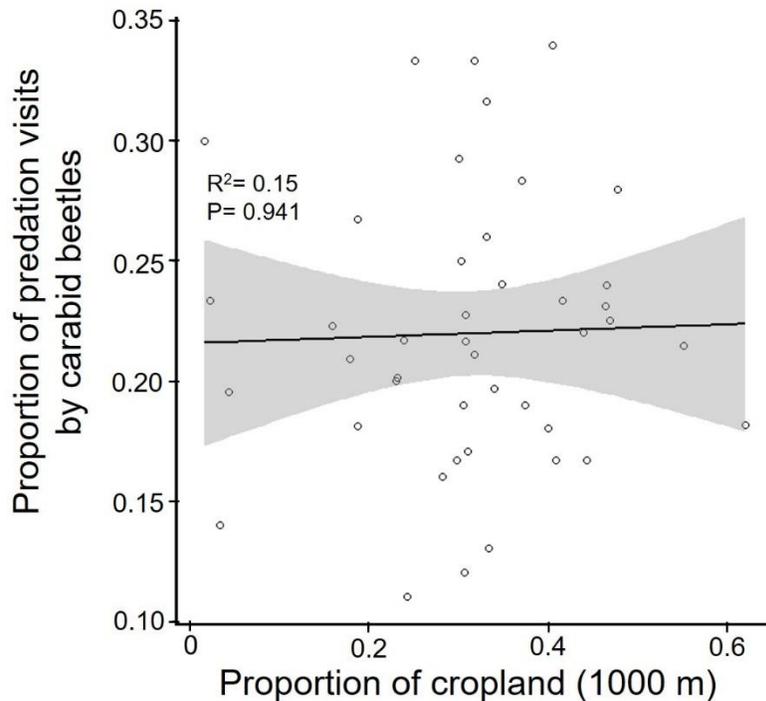


Fig. S3.3. Relationship between the proportion of the total predator visits to sentinel prey made by carabid beetles and the proportion of cropland in a 1000 m radius around the experimental plots. Each data point represents a single community (plot). Line depicts predicted trend from the linear mixed-effects model and associated 95% confidence intervals (gray shaded). Conditional coefficient of determination (R^2) and significance of fixed effects are shown. See Supplementary Methods S1 for additional details.

Supplementary Methods S3.2: Cluster analysis to separate ground beetle species based on body size

The 47 ground beetle species recorded during this study were classified into body size classes using a Ward's agglomerative hierarchical clustering algorithm (Murtagh and Legendre 2014). This approach clustered similar body size species based on a matrix of Euclidean distances, which is an efficient method to identify clusters based on minimum within-cluster variance without making an a priori determination of the number of clusters to generate (Gordon 1987). To define the optimal number of clusters (i.e. size classes), we used a silhouette analysis (Jackson et al. 2010). Significance of the resulting cluster arrangement was then estimated via multi-scale bootstrap resampling with 1000 replications (Suzuki and Shimodaira 2006). Analyses

were conducted using stats (i.e. hclust function), cluster (Maechler et al. 2019), and pvclust (Suzuki and Shimodaira 2015) packages.

Cluster analysis led to the definition of two body size classes: small (elytra length range: 1.5-6.2) and large-bodied species (elytra length range: 7.3-13.7 mm) (Fig S2). The probability that each cluster is supported by the data rather than being random is given by the approximately unbiased (AU) p-values based on the bootstrap replications (Suzuki and Shimodaira 2006). AU p-values indicated that clusters in the dendrogram are highly supported by the data ($P \leq 0.03$).

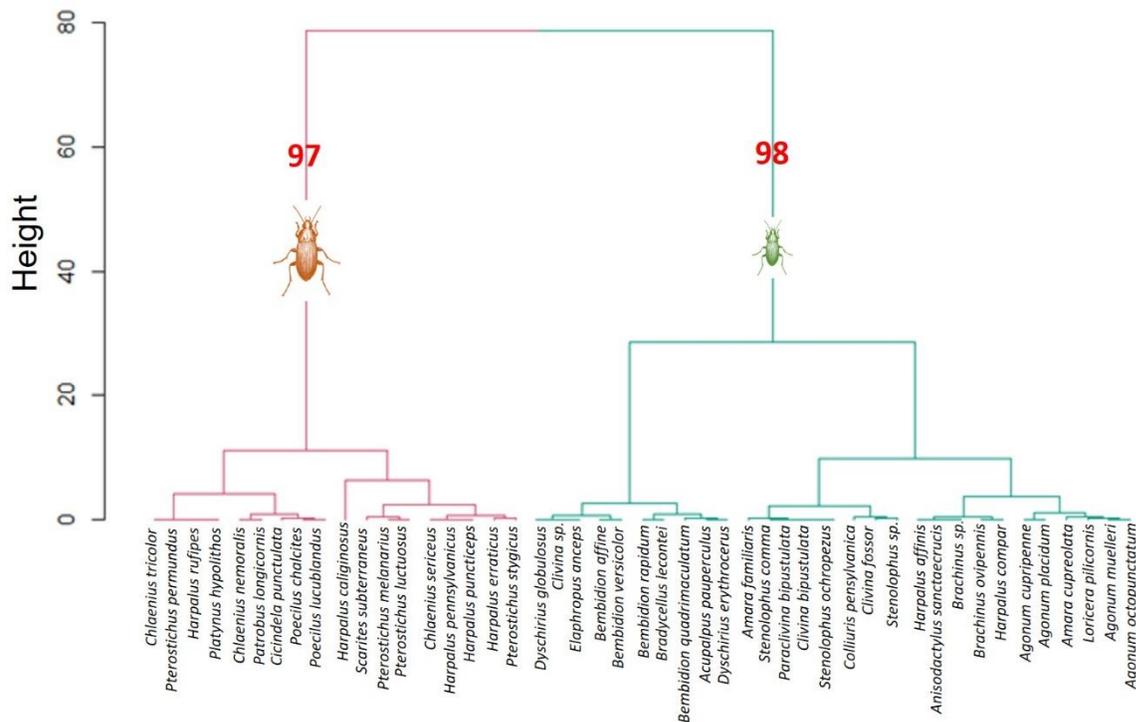


Fig. S3.4. Dendrogram of the agglomerative hierarchical clustering analysis separating clusters of ground beetle species based on body size. Cluster analysis separated species into two body size classes: large (n = 18) and small-bodied (n = 29) species. The height scale represents between-species Euclidean distance. Approximately unbiased (AU) probability values (numbers in red) for each cluster are indicated in the dendrogram. See Supplementary Methods S2 for more details.

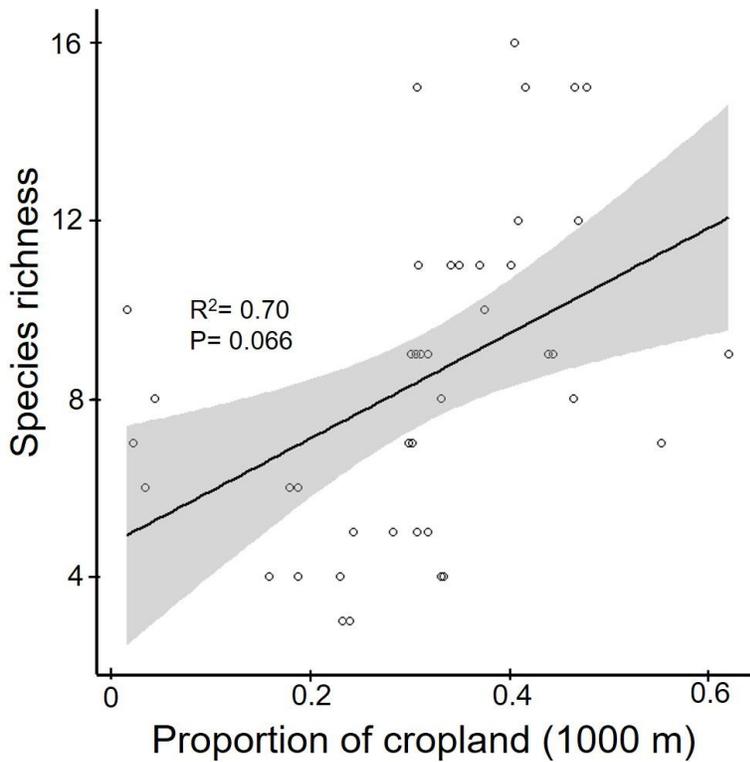


Fig. S3.5. Relationships between ground beetle species richness (i.e. number of species) and the proportion of cropland in a 1000 m radius around the experimental plots. Each data point represents a single community (plot). Line depicts predicted trend from the linear mixed-effects model and associated 95% confidence intervals (gray shaded). Conditional coefficient of determination (R^2) and significance of fixed effects are shown. See main text for more details.

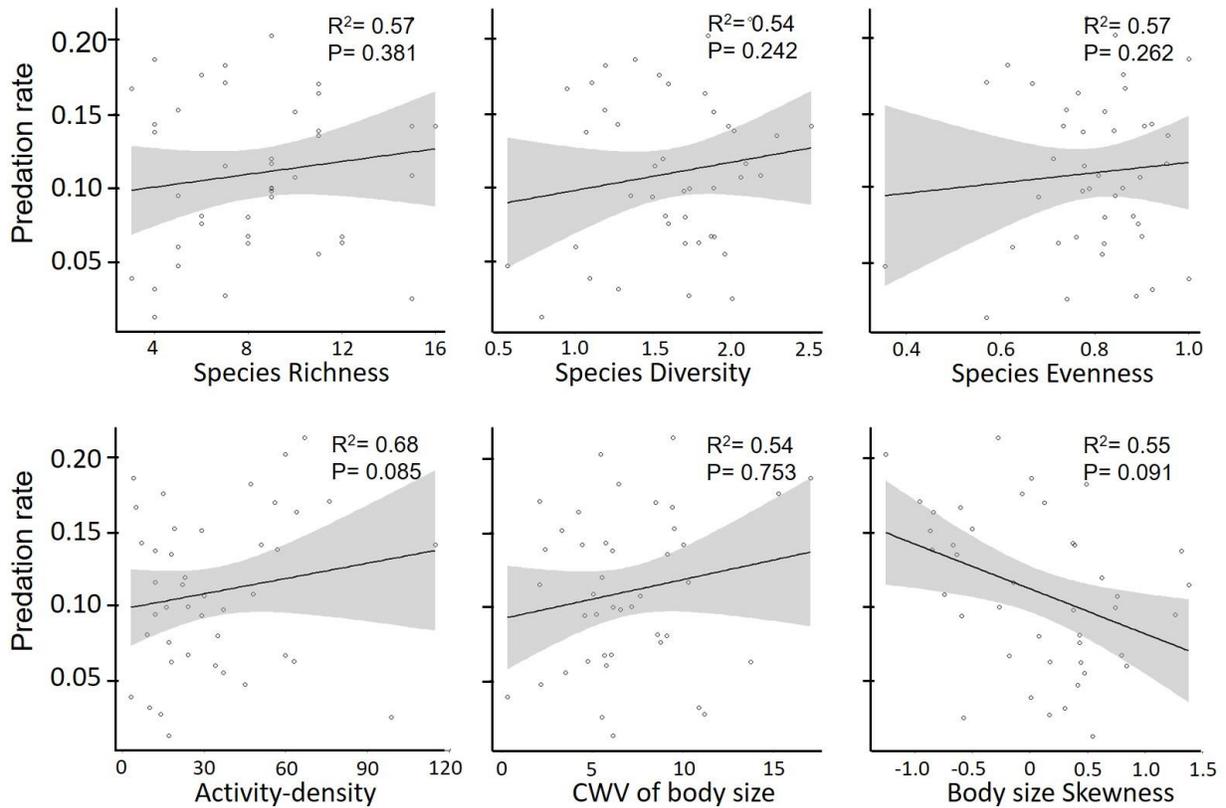


Fig. S3.6. Relationship between predation rates on sentinel diamondback moth pupae and different components of ground beetle community structure. Among the several components of predator community structure, we tested the effect of species richness (number of species), species diversity (Shannon-Wiener), species evenness (Pielou's evenness), activity-density, community weighted variance of body size (CWV), and body size skewness. Lines depict predicted trends from linear mixed-effects models and associated 95% confidence intervals (gray shaded). Conditional coefficient of determination (R^2) and significance of fixed effects are shown. See Table S4 for statistics.

Table S3.4. Statistical models for the effects of different components of ground beetle community structure and potential interactions with the proportion of cropland at the 1000 m spatial scale on predation rates on sentinel diamondback moth pupae. Dashed lines represent interaction terms not included in the final models because they were not significant ($P > 0.05$). The overall best model is bolded. The AICc values and AICc difference (ΔAICc) are given for each model. Models were selected based on second order Akaike Information Criterion (AICc).

Predictors	d.f.	F	P-value	AICc	ΔAICc
Species Richness (number of species)	1, 19	0.806	0.381	-112.084	11.091
Interaction (richness x cropland)	-----	-----	-----	-----	-----
Species Diversity (Shannon-Wiener)	1, 19	1.461	0.242	-116.472	6.703
Interaction (diversity x cropland)	-----	-----	-----	-----	-----
Species Evenness (Pielou's evenness)	1, 19	1.338	0.262	-118.461	4.714
Interaction (evenness x cropland)	-----	-----	-----	-----	-----
Activity-density	1, 19	3.303	0.085	-110.028	13.147
Interaction (activity-density x cropland)	-----	-----	-----	-----	-----
Community Weighted Mean of body size (CWM)	1, 19	9.194	0.006	-123.175	0
Interaction (CWM x cropland)	-----	-----	-----	-----	-----
Community Weighted Variance of body size (CWV)	1, 19	0.102	0.753	-111.054	12.121
Interaction (CWV x cropland)	-----	-----	-----	-----	-----
Body size Skewness	1, 19	3.179	0.091	-117.454	5.721
Interaction (skewness x cropland)	-----	-----	-----	-----	-----

REFERENCES

- Bousquet, Y. 2010. Illustrated Identification Guide to Adults and Larvae of Northeastern North American Ground Beetles (Coleoptera: Carabidae). Sofia-Moscow, Bulgaria: Pensoft Publishers.
- Dray, S., and Dufour, A. B. 2007. The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software* **22**: 1–20.
- Gordon, A.D. 1987. A review of hierarchical classification. *Journal of the Royal Statistical Society A*. **150**: 119–37.
- Grieshop, M.J., Werling, B., Buehrer, K., Perrone, J., Isaacs, R., and Landis, D. 2012. Big brother is watching: Studying insect predation in the age of digital surveillance. *American Entomologist* **58**: 172–182.
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., and Assmann, T. (2013) Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity* **7**: 195–205.
- Jackson, D.A., Walker, S.C., and Poos, M.S. 2010. Cluster Analysis of Fish Community Data: “New” Tools for Determining Meaningful Groupings of Sites and Species Assemblages. *American Fisheries Society Symposium* **73**: 503–527.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. (2019). cluster: Cluster Analysis Basics and Extensions. R package version 2.0.9.
- Murtagh, F., and Legendre, P. 2014. Ward’s Hierarchical Agglomerative Clustering Method: Which Algorithms Implement Ward’s Criterion?. *Journal of Classification* **31**: 274–295.
- Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**: 133–142.
- Pinheiro, J. C., and Bates, D. M. 2000. Mixed effects models in S and S-Plus. New York, NY, USA: Springer-Verlag New York.
- Suzuki, R., and H. Shimodaira. 2006. Pvclust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics* **22**: 1540–1542.
- Suzuki, R., and H. Shimodaira. 2015. pvclust. Hierarchical clustering with P-values via multiscale bootstrap resampling. R package version 2.0-0.

Zuur, A. F., Leno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. 2009. Mixed Effect Models and Extensions in Ecology with R. New York, NY, USA: Springer-Verlag New York.