# Landscape simplification reduces classical biological control and crop yield

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*Abstract.* Agricultural intensification resulting in the simplification of agricultural landscapes is known to negatively impact the delivery of key ecosystem services such as the biological control of crop pests. Both conservation and classical biological control may be influenced by the landscape context in which they are deployed; yet studies examining the role of landscape structure in the establishment and success of introduced natural enemies and their interactions with native communities are lacking. In this study, we investigated the relationship between landscape simplification, classical and conservation biological control services and importantly, the outcome of these interactions for crop yield. We showed that agricultural simplification at the landscape scale is associated with an overall reduction in parasitism rates of crop pests. Additionally, only introduced parasitoids were identified, and no native parasitoids were found in crop habitat, irrespective of agricultural landscape simplification. Pest densities in the crop were lower in landscapes with greater proportions of semi-natural habitats. Furthermore, farms with less semi-natural cover in the landscape and consequently, higher pest numbers, had lower yields than farms in less agriculturally dominated landscapes. Our study demonstrates the importance of landscape scale agricultural simplification in mediating the success of biological control programs and highlights the potential risks to native natural enemies in classical biological control programs against native insects. Our results represent an important contribution to an understanding of the landscape-mediated impacts on crop yield that will be essential to implementing effective policies that simultaneously conserve biodiversity and ecosystem services.

*Key words: agricultural landscape simplification; biological control; crop yield; ecosystem services;* Lygus lineolaris; *niche compression;* Peristenus digoneutis; *strawberry.*

## Introduction

Globally, conversion of natural lands to agricultural uses is one of the greatest threats to biodiversity and ecosystem function. Over the past century, the intensification of agricultural production practices has resulted in the simplification of agricultural landscapes and a decrease in the abundance and diversity of farmland plant, bird and insect communities (Koizumi et al. 2010, Chaplin-Kramer et al. 2011, Fischer et al. 2011, Batáry et al. 2012, Tscharntke et al. 2012, Lindborg and Eriksson 2014). In many cases, the species lost in simplified agricultural systems are important providers of ecosystem services including pollination (Steffan-Dewenter et al. 2001, Garibaldi et al. 2011) and biological control of pests (Chaplin-Kramer et al. 2011, Rusch et al. 2016). However, even in areas where agricultural practices are locally intensive, structural complexity at the landscape scale can allow for the maintenance of diverse communities of ecosystem service providers (Tscharntke et al. 2005, Gámez-Virués et al. 2015, Park et al. 2015). Thus,

understanding the role of landscape structure in mediating the delivery of ecosystem services is a critical step toward designing agricultural systems that capitalize on ecological processes to increase the quantity and stability of crop yields (Bommarco et al. 2013).

Although beneficial insects are often negatively impacted by landscape simplification (Thies et al. 2003, Bianchi et al. 2006, Chaplin-Kramer et al. 2011), pest populations generally benefit from reduced top-down control from natural enemies and reduced bottom-up control due to greater concentrations of crop host plants (Root 1973). In order to decrease pest pressure in agroecosystems, ecologically based management practices have focused on increasing the diversity and abundance of natural enemies. This can be achieved through conservation biological control, which aims to promote naturally occurring enemies, or by classical biological control in which exotic natural enemies are imported and released. Landscape composition is likely to influence the effectiveness of both classical and conservation biological control programs (Gurr and Wratten 1999, Landis et al. 2000). Many studies have shown effects of landscape composition on natural predator and parasitoid assemblies (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Shackelford et al. 2013, Veres et al. 2013); yet, we are

aware of only a few studies of landscape effects on the success of nonnative biological control agents (Gardiner et al. 2009, Woltz et al. 2012). Similar to native natural enemies, introduced biological control agents are likely to benefit from landscapes with overwintering habitat, floral resources and host reservoirs outside of the cropping system. For example, Pickett et al. (2009) credit the successful establishment of *Peristenus relictus* for the control of *Lygus hesperus* in California to the presence of wild vegetation in field margins, which may have provided alternative hosts and floral resources.

Landscape structure may also mediate the interactions between native and introduced natural enemies (Bowers and Dooley 1991, Didham et al. 2007). Exotic biological control agents can be expected to be more effective than native enemies in agricultural systems since they are introduced only when it is perceived that natives provide insufficient control of pest populations. Greater attack rates of the introduced enemy on the pest may lead to competition resulting in niche compression of the native enemies (MacArthur and Wilson 1967, Dickman 1986). Natural habitat remnants in agricultural landscapes may therefore serve as refuges, supporting populations of native enemies that spill over into crop habitats. Because landscapes with lower agricultural land cover tend to have more of these semi-natural refuge habitats, pest control is predicted to be greatest in these landscapes, as complementarity between native and introduced enemies is maximized (Cardinale et al. 2003).

Although landscape structure can impact the dynamics of the interactions between native and introduced enemies and their ability to provide biological control services, no studies have explicitly taken a landscape approach to evaluating the success of a classical biological control program. Furthermore, relatively few studies have linked landscape-mediated changes in natural enemy communities to changes in pest populations or more importantly to crop yields (Chaplin-Kramer et al. 2011, Liere et al. 2015); although demonstrating this link will be critical in designing and implementing ecologically informed agricultural practices (Bommarco et al. 2013). Using the ubiquitous crop pest *Lygus lineolaris* and its complex of native and introduced parasitoids, we investigated the relationship between landscape-scale agricultural simplification, classical and conservation biological control services and crop yield. We predicted that increasing proportions of agriculture in the landscape would lead to decreased attack rates on the pests, and increased pest densities. Therefore, crop yields on farms in simplified landscapes are expected to be lower than on farms with more natural habitat in the surrounding landscape.

## Materials and Methods

### Study area and sites

The study was conducted in central New York State, USA in the spring of 2012 in commercial strawberry fields. The region is characterized by a diversity of agricultural uses, including dairy, row crop, tree fruits, and vegetables with natural and semi-natural areas of deciduous forest, small woodlots, and old fields dispersed throughout. Using the natural variation in habitat composition, 11 farms in five counties representing a gradient in agricultural landscape simplification were identified (Appendix S1: Fig. S1). All farms included in the study were certified organic or used low-intensity management practices. Individual field sites on each farm were comprised of established fields of the most commonly grown strawberry variety in the area, Jewel.

Strawberry (*Fragaria × ananassa*) is an excellent system for understanding how landscape influences the impact of native and introduced natural enemies on pest control because the system contains closely related native and introduced natural enemies attacking the same host. The primary pest of strawberry, *L. lineolaris,* is an economically important pest of many high-value fruit and vegetable crops and also field crops throughout the United States. Although *L. lineolaris* is a native insect and its primary natural enemies are a complex of native parasitoids, *Peristenus pallipes* and *Peristenus pseudopallipes* (Hymenoptera: Braconidae)*,* the USDA introduced an exotic parasitoid in the same genus, *Peristenus digoneutis,* to the United States in the 1980s. The introduction of *P. digoneutis* by the USDA is a well-studied classical biological control program (Day et al. 1990, 2003, 2008, Day 1996, 2005, Lachance et al. 2001, Tilmon and Hoffmann 2003, Carignan et al. 2007, Day and Hoelmer 2012), and parasitism rates achieved by *P. digoneutis* in the field are well above those recorded for native parasitoids (Day 1996).

### Estimating pest densities

Each field was sampled for *L. lineolaris* three times approximately 1 week apart representing petal fall, green fruit, and ripe stages of strawberry fruit maturation. We were unable to obtain samples from three farms during the petal fall stage and one farm during the green fruit stage. Nymphs are the predominate life stage during this time period. *L. lineolaris* nymphs were collected from two rows along a 20-m transect using a backpack vacuum sampling device (Echo ES 230 Shred 'n Vac, Lake Zurich, Illinois, USA). The device was applied to the foliage 50 times along each row before the contents of the sample were immobilized with $CO_2$ gas and all *L. lineolaris* nymphs were collected and stored in 95% ethanol.

### Parasitism assay

Random samples of 24 nymphs from each sampling period at each site were selected for parasitism assays. In some cases fewer than 24 nymphs were collected in a sampling period. In this case, all collected nymphs for the period were processed. Diagnostic PCR assays were used to

simultaneously estimate parasitism rates and parasitoid species identity, as they are faster and more accurate than rearing or dissection (Tilmon et al. 2000, Ashfaq et al. 2004). DNA from nymphs was extracted using an abbreviated chlorophorm : isoamyl alcohol protocol developed by Tilmon and Hoffmann (2003). DNA extractions along with negative controls were amplified using *Peristenus* species-specific primers (see Appendix S1) as in Gariepy et al. (2005). Using this method, species-specific forward primers are combined with a genus-specific reverse primer to amplify a region including ITS1 and ITS2. Presence of an amplicon indicates parasitism and the length of the fragment indicates parasitoid species identity.

### Estimating strawberry yield

To measure the impact of *L. lineolaris* on yield at each site, 30 secondary fruits from eight of the 11 sites were harvested when ripe and weighed. At the three remaining sites, grower harvesting prevented us from obtaining fruit samples. A typical strawberry inflorescence is composed of a single primary fruit (king berry), a pair of secondary fruit, four tertiary fruit, and sometimes additional quaternary fruit. Secondary fruit were used, as they are less prone to frost damage than primary fruit and due to their later development are more susceptible to damage from *L. lineolaris* nymph feeding.

Strawberries are an aggregate accessory fruit composed of as many as 300 achenes on a primary fruit and 200 on a secondary fruit (Webb et al. 1978). *L. lineolaris* nymphs and adults feed on developing achenes leading to a failure in development of the surrounding tissues. The mass of a fruit is highly correlated with the number of developed undamaged achenes (Webb et al. 1974). Fruits with a high percentage of damaged achenes develop with major malformations that reduce overall yield and marketability (Schaefers 1980).

### Landscape analysis

Landscape simplification was assessed by measuring the proportion of land in annual agricultural (row and vegetable crops), perennial agriculture (orchards, vineyards, forage, and pasture), forest, and open semi-natural covers (fallows, old fields, and wetlands) in circular areas around each of the field sites using the 2012 National Agricultural Statistics Service Cropland Data Layer for New York (USDA 2012) in ArcGIS 10.1 (ESRI, Redlands, California, USA). Urban habitats comprised only 1% of land cover and were therefore not considered in the analysis. Corn, soy, and wheat were the dominant annual agricultural land covers (27%) while pasture (20%) and alfalfa (7%) were the dominant perennial agricultural covers. In order to determine which scale best predicted the abundance and parasitism of *L. lineolaris* nymphs, multiple scales with radii of 250, 500, 750, and 1,000 m were classified. In the study region, the proportion of annual agriculture is negatively related to the cover of open semi-natural habitats ($r = -0.76$, $P = 0.003$), perennial agriculture ($r = -0.66$, $P = 0.018$), and forest cover ($r = -0.63$, $P = 0.026$) while open semi-natural cover is positively correlated with the proportion of perennial agriculture ($r = 0.52$, $P = 0.08$) and forest ($r = 0.61$, $P = 0.035$). Additional information on land covers and their correlations are provided in Appendix S1.

### Statistical analyses

To determine the landscape scale most predictive of parasitism rates by *Peristenus* wasps as well as the abundance of *L. lineolaris* nymphs, we used the dredge function (R package MuMIn; Bartoń, 2013) to construct mixed effects models at each scale (250–1,000 m) using the nlme package (Pinheiro et al., 2014). Minimum adequate models for each response variable (parasitism and nymph abundance) were limited to one scale per model based on second-order Akaike Information Criterion corrected for sample size ($AIC_c$). The cover with the lowest $AIC_c$ score was selected when two or more scales for a cover were equally likely. The sampling period (petal fall, green fruit, ripe fruit) was included in all models as a fixed effect and sampling period nested within farm was included in all models as a random effect. The most predictive scale for each land cover identified in this analysis was then used in further analyses.

The effect of landscape at the most predictive scale on parasitism of *L. lineolaris* nymphs by *Peristenus* wasps was evaluated with a manual hurdle model, which first assessed the effect of landscape on the presence or absence of parasitism and then, for sites where parasitism occurred, evaluates the relationship between landscape and parasitism rates. Generalized linear mixed models (GLMM) were fit using the R package glmmADMB (Skaug et al. 2016) with the most predictive landscape scale as the predictor variable and sampling period nested within farm as random effects. A negative binomial error distribution was used in the model predicting presence or absence of parasitism while a Gaussian error distribution was used in the model predicting parasitism rate.

The association of landscape at the most predictive scale on *L. lineolaris* nymph abundance was evaluated with a generalized linear mixed model with a Poisson error structure. Sampling period, proportion of agriculture at the most predictive scale, and their interaction were included as fixed effects with a random effect of farm. The relationship between nymph abundance and parasitism rates was also evaluated with a Poisson GLMM with parasitism rate as the response variable and nymph abundance, sampling stage, and their interaction as fixed effects with a random effect of farm.

The impact of *L. lineolaris* abundance on strawberry yield was evaluated with simple linear regression for each sampling period separately and for the average abundance between petal fall and green fruit sampling periods as this time period represents the time when strawberries would have been most susceptible to *L. lineolaris* feeding.

Additionally, we evaluated the direct effects of landscape simplification on yield using a simple linear model with average fruit mass as a response variable and land cover at the most predictive scale for *L. lineolaris* nymphs.

Spatial independence of model residuals was evaluated for each model by means of the Moran's *I* test. Evidence of spatial autocorrelation was not found in any model (Table S3).

<div style="text-align:center">RESULTS</div>

A total of 1,683 *L. lineolaris* nymphs were collected from strawberry farms in 2012, from which 766 nymphs were assayed for parasitism by *Peristenus* wasps by amplification of species-specific DNA fragments. Parasitism rates ranged from 0% to 46.7%. For all nymphs found to be parasitized, only *P. digoneutis* was identified, with no evidence of parasitism by the native wasp *P. pallipes*. Parasitism rates were zero for nearly one-half of all collection events. Parasitism rates were best predicted by land covers at the smallest scales (Appendix S1: Table S4). Greater proportions of annual agriculture in the landscape at the 500-m scale were associated with a lower probability of observing a parasitism event ($z_{11} = -1.94$, $P = 0.052$, Appendix S1: Fig. S5). Across sites where parasitism did occur, increasing amounts of open semi-natural habitat surrounding farms were associated with an increase in parasitism rates ($F_{1,7} = 9.38$, $P = 0.01$, Fig. 1) independent of sampling period. A competing model with forest cover at the 250-m scale ($\Delta AIC_c = 0.72$) was also associated with increased parasitism rates ($F_{1,7} = 10.78$, $P = 0.01$, Fig. 2).

*Lygus lineolaris* nymph abundance was also influenced most strongly by the proportion of semi-natural land covers but at the 750-m scale (Appendix S1: Table S5). Nymph abundance varied across sampling periods ($F_{1,2} = 85.84$, $P = 0.01$) but was negatively associated with increasing proportions of semi-natural habitats in



FIG. 2. Average number of *L. lineolaris* nymphs collected from strawberry fields decrease with respect to the proportion of open semi-natural habitats at 750 m surrounding the sampling location within each strawberry field.

the landscape across all sampling periods ($z = -4.255$, $P > 0.001$; Fig. 2). Parasitism rates were not associated with nymph densities at petal fall and green fruit sampling periods although there was a positive relationship between nymph density and parasitism rates during the ripe fruit stage when *L. lineolaris* abundance was highest ($z = 8.74$ $P > 0.001$).

Sites with greater *L. lineolaris* nymph densities at the petal fall and green fruit sampling periods tended to have lower yields than sites with fewer nymphs during these intervals ($F_{1,6} = 4.61$ $P = 0.07$, Fig. 3). However, there was no effect of nymph density on yield during the ripe fruit sampling period ($F_{1,6} = 0.13$ $P = 0.73$). Additionally, yield was negatively associated with landscape composition such that farms with greater proportions of semi-natural habitats in the surrounding landscape had overall higher yields than farms in more complex landscapes ($F_{1,6} = 20.75$ $P = 0.003$, Fig. 4).
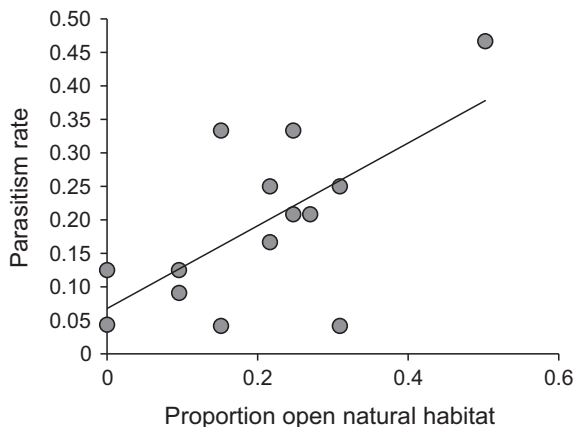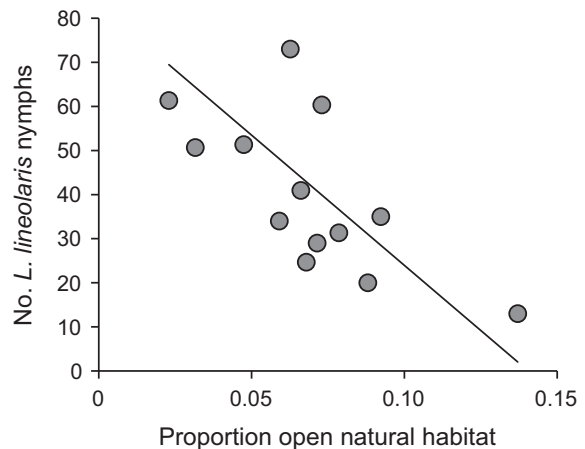


FIG. 1. Parasitism rates of *Lygus lineolaris* nymphs by *Peristenus digoneutis* are positively related to the proportion of open semi-natural habitats at 500 m surrounding the sampling location within each strawberry field.
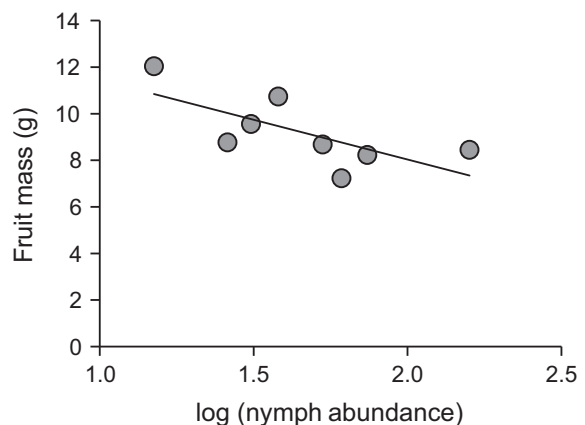


FIG. 3. Average strawberry fruit mass is negatively related to the log of *L. lineolaris* nymph abundance in the time interval including the petal fall and green fruit sampling periods.
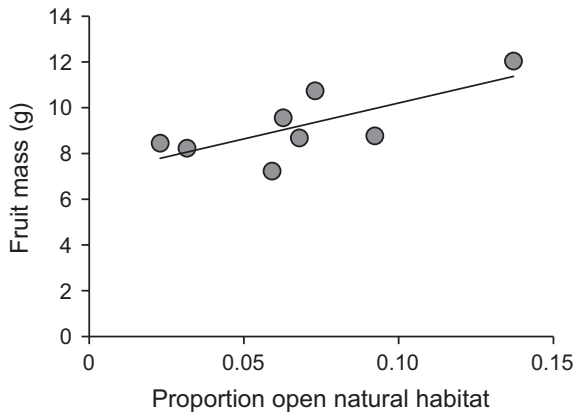
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Fig. 4. Average mass of strawberry fruits is positively related to the proportion of agricultural land use at 750 m surrounding the sampling location within each field.

## DISCUSSION

Our study reveals that loss of natural habitats within the landscape associated with an increase in annual agricultural land uses has opposing effects on pest and natural enemy populations leading to a decrease in the effectiveness of classical biological control. Parasitism rates of the introduced wasp decreased while pest numbers increased with greater proportions of agricultural land uses in the surrounding landscape. Although the importance of landscape context in mediating pest control services has been widely recognized (Thies and Tscharntke 1999, Bianchi et al. 2006, Rusch et al. 2013, 2016) our findings reveal that these same ecological processes can impact classical biological control programs. Our results add a further dimension to this body of research by demonstrating that these effects translated into consequences for strawberry yield. Finally, we show dominance of the introduced parasitoid, *P. digoneutis*, and the complete absence of native wasps attacking *L. lineolaris* nymphs in strawberry fields, suggesting that a non-target effect of this introduced parasitoid may have been to displace its native congener.

Increases in annual agriculture surrounding strawberry fields was associated with a decrease in the likelihood of parasitism. When parasitism occurred, sites with fewer permanent natural habitats in the landscape had decreased rates of *L. lineolaris* parasitism by *P. digoneutis*. Parasitism rates were best predicted by smaller spatial scale than those that were most important for predicting *L. lineolaris* nymph densities, likely reflecting differences in the normal foraging ranges of *P. digoneutis* and of female *L. lineolaris* as they move from overwintering habitats into crop fields (Khattat and Stewart 1980, Fleischer et al. 1988, Bancroft 2005). Because parasitoids respond at smaller spatial scales than their hosts, small scale management on farms may be successful at increasing parasitism rates.

Higher rates of parasitism in landscapes with greater proportions of permanent natural habitats likely reflect the increased availability of resources for parasitoids, such as nectar and availability of *L. lineolaris* population reservoirs outside of the cropping system. In our study, open natural habitats were comprised primarily of fields that had been abandoned from agriculture for >10 yr and included a diverse mix of herbaceous plants and shrubs. Based on detailed studies of the reproductive biology of *P. digoneutis*, Haye et al. (2005) report nectar feeding to be instrumental in achieving high rates of parasitism as newly emerged female wasps have very few mature eggs and were not observed to engage in host feeding. Pickett et al. (2009) note the presence of weedy field margins as a factor in the successful establishment of closely related *P. relictus* in California strawberry.

In our study, molecular assays revealed that all parasitism events of *L. lineolaris* nymphs were by *P. digoneutis*. No instances of parasitism by the native *P. pallipes* were found despite the fact that previous studies of parasitism rates of *L. lineolaris* in the same region, and in some cases at the same sites, found *P. pallipes* to be ubiquitous (Tilmon and Hoffmann 2003). These results may represent a culmination of the observed trend in reduced parasitism by the native wasps following the introduction and range expansion of *P. digoneutis* (Day 2005). Prior to the establishment of *P. digoneutis*, parasitism rates by *P. pallipes* often reached 25% (Carignan et al. 2007). Tilmon and Hoffmann (2003) reported lower parasitism rates by *P. pallipes* in eastern New York strawberries (3.7%) compared to western New York (10.5%) where *P. digoneutis* was less well established. More recently, parasitism rates of *L. lineolaris* in New Jersey strawberry averaged 30%, with up to 98% of parasitism events by *P. digoneutis* (Day and Hoelmer 2012). Although parasitoid populations may fluctuate from year to year, it is unlikely that *P. pallipes* would be absent from all sites surveyed across the region in any given year. This result, combined with evidence from the literature of declines in the native species since the introduction of the nonnative, supports the hypothesis of competitive exclusion.

Classical biological control has traditionally been considered as a safe and effective means of pest control, particularly for invasive pests. However, due to the greater number of pre-existing interactions between species, classical biological control of native insects is more risky than for nonnatives as loss of native enemies is more likely. Such non-target effects of introduced parasitoids have been reported in other systems (Bennett 1993). Loss of alternative natural enemies from the system is expected to result in a reduction in functional complementarity and the ability of the community to respond to disturbance, potentially leading to a reduction in the resilience of biological control services. Although *P. digoneutis* has become the dominant parasitoid in agricultural habitats, little is known about interactions between *Peristenus* species in non-crop habitats. As a response to competition, *P. pallipes* may have undergone niche compression (MacArthur and Wilson 1967) and stable populations of *P. pallipes* may still persist in other habitats such as

natural habitats or fallow fields (Bahlai et al. 2015). In this case, functional complementary between parasitoid species attacking *L. lineolaris* in different habitats may maintain higher levels of pest suppression than one species alone. Alternatively, populations of *P. digoneutis* subsidized by host populations in agricultural habitats may spill over into natural habitats resulting in increased pressure on native parasitoid populations (Frost et al. 2015). Future studies should therefore evaluate the levels of parasitism and parasitoid community composition of *L. lineolaris* in non-crop habitats. Studies should also focus on evaluating parasitism of *L. lineolaris* in later generations when *P. digoneutis* may compete with later season parasitoids of *L. lineolaris* such as *P. pseudopallipes.*

During the petal fall and green fruit sampling periods, *L. lineolaris* nymph abundances in strawberry were lower in landscapes with greater proportions of natural habitats and higher parasitism rates. These results suggest that *P. digoneutis* may be suppressing *L. lineolaris* populations in these landscapes. Other natural enemies, including predators of *L. lineolaris,* are more likely to be abundant in more complex landscapes as well (Chaplin-Kramer et al. 2011). Farms with greater nymph abundances during the petal fall and green fruit sampling periods had smaller fruits at harvest while nymph densities during the last sampling period, when fruit were nearly ripe, were not correlated with fruit mass at harvest. This is to be expected as fruit that has attained final size are less susceptible to *L. lineolaris* feeding damage (Handley and Pollard 1993). These results suggest that farms in simplified agricultural landscapes with greater nymph abundances are likely to experience overall lower yields. Indeed, we found a negative relationship between the proportion of agriculture in the landscape at 500 m and the average mass of strawberry fruits at harvest. Although damage from *L. lineolaris* feeding was not directly measured in this study, it is expected that *L. lineolaris* feeding is the primary factor leading to yield loss as damage to fruit from other pests was not observed in any of our samples. Poor pollination may also have contributed to reduced yields on farms in highly agricultural landscapes as strawberry is pollinated by a diverse native bee community, which is negatively impacted by agricultural simplification (Connelly et al. 2015). To better understand the relative contributions of pollination and biological control to strawberry yield, we suggest additional studies that independently manipulate pollinator visitation and *L. lineolaris* nymph densities.

Managing ecosystem services to agriculture requires a landscape scale approach (Tscharntke et al. 2005, 2012), although landscape context has rarely been considered in classical biological control programs. Landscape structure is known to influence natural enemy abundance and pest control in other agricultural systems (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Rusch et al. 2016). As members of higher trophic levels, parasitoids are expected to respond more strongly to landscape context than their hosts (Thies et al. 2003) since parasitoids with small

foraging ranges and those that require alternative host and floral resources are filtered from agriculturally simplified landscapes (Gámez-Virués et al. 2015). Although landscape-mediated changes in natural enemy communities and herbivore densities are expected to translate into lower crop damage and greater yields in complex landscapes, few studies have evaluated either of these outcomes. Thus, our results represent an important contribution to an understanding of the landscape-mediated impacts on crop yield that will be essential to implementing effective policies that simultaneously conserve biodiversity and ecosystem services. At the landscape scale, policies that promote land use diversity by incorporating natural and semi-natural land uses such as forests, parks, old fields, and residential and urban areas, are expected to enhance the delivery of biological control services and support crop productivity in nearby agricultural lands. At smaller scales, it is possible that biological control services in simplified agricultural landscapes could be improved by the incorporation of hedgerows or flowering strips that provide increased floral diversity at the field scale (Blaauw and Isaacs 2015, Sidhu and Joshi 2016).

Our findings have particularly important implications for the practice of classical biological control. Our results indicate that introduced natural enemies are more likely to be successful if landscape context is considered in their establishment. Of the 34% of classical biological control agents that have established in the period between 1890 and the 1960s, the rate of success was higher among those that were established in more stable compared to disturbed habitats (Hall et al. 1980). Our results suggest that even in the absence of native natural enemies, conserving natural habitats within agricultural landscapes will promote biological control and crop yield. If exotic natural enemies must be released in agriculturally simplified landscapes, candidate species with life histories that are less dependent on non-crop habitats should be favored or practitioners should consider supplementing these resources with small-scale features such as hedgerows or wildflower plantings (Pickett et al. 2009). Finally, practitioners should take into consideration interactions between introduced and native enemies when developing classical biological control programs, particularly for those against native pests.

Monitoring of *P. digoneutis* since its introduction has allowed for insights into its spread, effect on populations of the target pest and its impact on native insect communities (Tilmon and Hoffmann 2003, Day 2005, Day et al. 2008). Although it was initially hypothesized that reductions in *L. lineolaris* populations in source crops like alfalfa would lead to reduced damage in high value crops like strawberry, our study is the first to report an indirect relationship between high levels of parasitism by *P. digoneutis* and greater yield on strawberry farms. Furthermore, we report a strong negative association between landscape simplification and crop yield. Our study sheds new light on the importance of landscape context in mediating the success of classical biological control programs.

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