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Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape

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ARTICLE INFO

Article history:

Received 10 June 2013

Received in revised form 14 March 2014

Accepted 15 March 2014

Keywords:

Agriculture

Pest control

Natural enemies

Restoration

Conservation biological control

Ecosystem services

ABSTRACT

Within-farm habitat enhancements such as hedgerows could aid pest control in adjacent crops; however, there is little information on whether small-scale restoration impacts pests and natural enemies, and crop damage, and how far effects may extend into fields. We compared restored, California native perennial hedgerows to unenhanced field edges consisting of commonly occurring semi-managed, non-native weeds. Pest and natural enemy communities were assessed in both edge types and into adjacent processing tomato fields. Using sentinel pest eggs, pest control was quantified, and pest pressure and crop damage was compared between field types. Economically-important pests were fewer and parasitoid wasps were more abundant in hedgerows than weedy crop edges. There was no difference in predatory arthropod abundance between edge types, but there was greater predator richness in hedgerow than weedy edges. Predatory lady beetles were more abundant and aphids were lower in fields with hedgerows, up to 200 m into fields, the maximum extent of observations. Fewer of the fields adjacent to hedgerows reached threshold pest levels requiring insecticide application. Benefits of hedgerows to pest control from parasitism extended to 100 m but not 200 m into fields. Farm-scale hedgerow restoration can provide pest control benefits up to 100 or 200 m into fields and multiple hedgerows around fields could enhance pest control throughout entire fields, reducing the need for chemical pest control.

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1. Introduction

There is growing evidence showing that more complex or diversified landscapes that have high proportions of non-crop habitat such as forests, field margins, and wetlands, enhance natural enemy abundance and diversity in crop areas (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). The evidence is less clear as to whether greater habitat complexity leads to greater pest suppression in crops (But see, Meehan et al., 2011), the ultimate goal for integrated pest management (Kremen and Miles, 2012).

In addition, there is little information on whether local diversification is effective for promoting pest suppression in crops (Griffiths et al., 2008). A recent meta-analysis of studies on within-farm diversification schemes found that diversified crops had enhanced natural enemy populations, greater pest suppression, and lower crop damage (Letourneau et al., 2011). However, they found that plant diversification within fields reduced primary crop

yield. Diversification on edges, mainly through addition of floral resources, enhanced natural enemy abundance and parasitism in crops; yet there are few studies in this category and no studies that assessed crop damage and pest control in relation to diversification at field edges.

Recently, Chaplin-Kramer and Kremen (2012) showed that local diversification within fields (polyculture) and/or around field (hedgerow) sources, can enhance natural pest control, compensating for low-complexity at a landscape level in some situations. It is vital to assess if such small, within-farm diversification strategies can impact pest suppression in intensive agricultural landscapes; because, while growers have little control over diversification at a landscape scale, they can implement local within-farm diversification (Morandin and Kremen, 2013).

Crop edge or hedgerow enhancement, as opposed to diversification within fields (whether intercropping or non-crop diversification), can utilize land that is not suitable for farming, taking little or no land from crop production, resulting in little or no reduced yield. However, it remains unclear whether restoration of a single hedgerow and other small-scale, local restoration strategies can compensate for low complexity at the landscape scale and how far benefits of edge restoration may extend into adjacent fields.

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Uncertainty as to how hedgerow establishment will alter pest and natural enemy insect communities, and ultimately pest control and crop yield, remain a major barrier to landowners' willingness to devote time and money to hedgerow restorations and other CBC strategies on their farms (Griffiths et al., 2008; Stamps et al., 2008).

We examined pest and natural enemy arthropod abundance and diversity in Californian native perennial hedgerows of flowering shrubs and grasses that had been planted on field borders in an intensive agricultural landscape to enhance beneficial insect populations and decrease weeds (Bugg et al., 1998). We assessed natural enemy and pest abundance and diversity into crops adjacent to hedgerows or weedy, semi-managed field edge habitats, conducted pest control experiments, and assessed crops for pest pressure and crop damage. We asked four main questions by comparing crop fields with hedgerows versus weedy semi-managed field edges: 1. Do hedgerows increase natural enemy abundance and diversity in field edges and adjacent crops? 2. Are pest populations lower in field edges and adjacent crops with hedgerows? 3. Is pest control enhanced and crop damage reduced in fields with hedgerows? and 4. If so, to what distances do changes in abundances, pest control, and crop damage extend into fields with hedgerows relative to crops with weedy edges?

2. Materials and methods

This study was conducted in Yolo County in California's Sacramento Valley during the 2009 and 2010 growing seasons. The study area is intensively farmed, primarily with rotational field crops including wheat, processing tomato, alfalfa, and seed crops such as sunflower and safflower.

Hedgerow plantings approximately 7 m wide were established at our study sites in 1996–2003 and were comprised of a row of native perennial shrubs, 305–550 m long, bordered by native perennial grasses. Plant species composition for each site varied somewhat but all contained California buckwheat (*Eriogonum fasciculatum foliolosum*), California lilac (*Ceanothus griseus*), California coffeeberry (*Rhamnus californica tomentella*), coyote brush (*Baccharis pilularis*), elderberry (*Sambucus mexicana*), and toyon (*Heteromeles arbutifolia*). These plants were selected because they are drought-tolerant, native California shrubs that are known to provide floral resources for natural enemy insects, and have successive and overlapping bloom periods (Bugg et al., 1998; Long et al., 1998).

Three-meter wide strips of native perennial grasses were planted along one or both sides of the hedgerow to help suppress weeds and create overwintering habitat for natural enemies; species included purple needlegrass (*Nassella pulchra*), nodding needlegrass (*N. cernua*), California onion grass (*Melica californica*), one-sided bluegrass (*Poa secunda*), blue wildrye (*Elymus glaucus*), and creeping wildrye (*Leymus triticoides*). In some sites however, few grasses remained, having been outcompeted by weeds. The primary herbaceous weeds occurring in hedgerows were mustard (*Brassica* spp.), field bindweed (*Convolvulus arvensis*), mallow (*Malva parviflora* and *neglecta*), and bristly oxtongue (*Picris echioides*), and varied among sites.

Within each year we chose hedgerow sites that were adjacent to processing tomato fields, one of the most economically important and common crops in the region, in order to assess pests of tomato and their natural enemies, crop damage, and pest control into fields. For each hedgerow site, we selected a matching control site with a weedy, semi-managed field edge habitat adjacent to a processing tomato crop with a similar planting date, located 1–3 km away. This design promoted independence of pest and natural enemy communities at hedgerow and control sites, while allowing both treatments to span the same environmental conditions across the

region. We attempted to get as many control fields with the same operators as hedgerow fields in order to minimize differences in pest control decisions between the two treatments, and were able to obtain half. We chose to compare the hedgerows to this type of semi-managed weedy field margin because it is the most prevalent edge type for crops in our region.

In 2010, two of the hedgerows were the same as in 2009; in one case the same field was used both years and in one case the field on the opposite side of the hedgerow was used (sites dictated by where the tomato crop was planted). Two control edges also were the same in 2009 and 2010, with one field being the same between years and one being on the opposite side of the field edge. Therefore, there were six unique hedgerows and six unique control edges over the two years of the study. We digitized and categorized land in a 1.5 km radius around each site using 1 m resolution orthophotos from the National Aerial Imagery Program (www.fsa.usda.gov/FSA) in ArcGIS (ESRI, 2009). At all sites, at least 85% of land in a 1.5 km radius around the center of the site was annual rotational crops with some smaller areas of orchard crops.

Pest and natural enemy arthropods were assessed in hedgerow and control sites ('sites' herein refers to edges and adjacent crops) four times (sample rounds) during each season with approximately one month between sample rounds, from early May until early August. This time frame spans the summer processing tomato production in our region.

2.1. Sweep samples

Sweep samples were taken four times during each season. A sweep sample consisted of 10, 180° sweeps with a 40 cm diameter net. Two samples were taken in the vegetation, 50–100 m from each end of the hedgerow or control edge (depending on edge length), and two at the center, for a total of six sweep samples at each site and sample round. Sweep samples were taken only when temperatures were $\geq 18^\circ\text{C}$, winds $\leq 2.5\text{ m/s}$ and skies were clear, and were always conducted at a hedgerow and its paired control site on the same day. At hedgerow sites, sweeps were taken into the native plant vegetation. Sweep samples were only conducted at edges of fields (hedgerows and weedy controls) and not in fields due to the potential to damage crop plants with this sampling method. We employed different methods to sample insects into tomato fields (see below) and used these methods in the edges as well.

After each sweep sample, insects and any vegetation in the net were carefully transferred from the net to a sealed and labelled bag, and put into a cooler. At the end of the field day, bags were put into a freezer for later processing at which time all insects $\geq 0.5\text{ mm}$ (plus mites and spiders) were removed from bags and transferred to centrifuge tubes with 70% ethanol. Insects were identified that were of economic importance to crops in our region. Identification was to species or higher taxonomic levels (Table 1).

2.2. Sticky card samples

Yellow "Sticky strip" 7.6 cm \times 12.7 cm sticky cards (Bioquip) were set out at sites four times each season. Unlike sweep samples, sticky cards could be used on edges and into fields and therefore could provide data in both locations. At each sample round, two sticky cards were placed at each of three field edge locations and along each of two transects into fields, at 10, 100, and 200 m from field edges, 100–200 m apart depending on field size, for a total of six sticky cards along field edges and six in fields. Sticky card wire holders (Bioquip) were used to hold cards above or adjacent to vegetation at all sites except where they hung from hedgerow shrubs with metal shower hangers. After seven days, sticky cards were collected, individually wrapped in plastic wrap, labelled, and put into freezers for later processing.

Table 1

Pest and natural enemy insects collected in hedgerow and control sites and adjacent tomato fields in 2009 and 2010. The majority of insects were categorized into groups listed under 'Identification level'; however, some specimens on sticky cards were identified only to 'Type' or 'Group'.

Type	Group	Identification level	Species or higher order present in study area	
Parasitoid	Aphidiidae	Aphidius	<i>Aphidius</i>	
		Chalcidoidea	Encyrtidae	Encyrtidae
		Mymaridae	Mymaridae	
		Pteromalidae	Pteromalidae	
		Trichogrammatidae	<i>Trichogramma</i>	
	Scelionidae	Scelionidae	Scelionidae	
		Tachinidae	Tachinid fly	Tachinidae
	Other parasitoids	Braconidae	Braconidae	
		Ceraphronoidea	Ceraphronoidea	
		Chrysoidea	Chrysoidea	
		Cynipoidea	Cynipoidea	
		Ichneumonidae	Ichneumonidae	
	Pest	Aphid	Aphid	Aphidoidea
Flea beetle		Flea beetle	<i>Phyllotreta</i> , <i>Epitrix</i>	
Leafminer		Leafminer	<i>Liriomyza</i>	
Lygus bug		Lygus bug	<i>Lygus</i>	
Cucumber beetle		Spotted cucumber beetle	<i>Diabrotica undecimpunctata</i>	
Stink bug		Conspere stink bug	<i>Euschistus conspersus</i>	
		Red-shouldered stink bug	<i>Thyanta pallidivirens</i>	
Weevil		Weevil	Curculionoidea	
Predator		Lady beetle	Convergent lady beetle	<i>Hippodamia convergens</i>
			Mealybug destroyer	<i>Cryptolaemus montrouzieri</i>
	Parenthesis lady beetle		<i>Hippodamia parenthesis</i>	
	Seven-spotted lady beetle		<i>Coccinella septempunctata</i>	
	Spidermite destroyer		<i>Stethorus picipes</i>	
	Twicestabbed lady beetle		<i>Chilocorus orbus</i>	
	Mantid		Praying mantid	Mantidae
	Neuropteran	Green lacewing	<i>Chrysopa</i> , <i>Chrysoperla</i>	
		Snake fly	Raphidioptera	
	Predatory beetle	Collops beetle	<i>Collops</i>	
		Rove beetle	Staphylinidae	
		Soldier beetle	Cantharidae	
	Predatory bug	Big-eyed bug	<i>Geocoris</i>	
		Damsel bug	<i>Nabis</i>	
		Leafhopper assassin bug	<i>Zelus renardii</i>	
	Predatory thrips	Minute pirate bug	<i>Orius</i>	
		Banded thrips	<i>Aeolothrips</i>	
Spider	Spider	Araneae		

Sticky cards were examined by dividing the cards into five, 1.9 cm strips (corresponding with the width of view under our dissecting microscopes at the lowest magnification) and identifying and quantifying insects on both sides of two end and middle strips. Insect identification level was similar to identification for sweep specimens (Table 1) except parasitoid microwasps were not identified further due to difficulty of manipulating and identifying specimens on sticky cards.

2.3. Visual assessment of field pests, natural enemies, and crop damage

We assessed pest and natural enemy insects in fields and crop damage using tomato crop assessment protocols outlined in the University of California Integrated Pest Management Guidelines (UC IPM) (<http://ipm.ucdavis.edu>). In late May each year, when the tomato plants were at flowering and early fruit stage, we assessed leaves for pests, primarily potato aphids (*Macrosiphum euphorbiae*).

We also recorded the presence of any other pests or pest eggs and natural enemy insects as described on the UC IPM site. This protocol was applied three times over each season. During the second and third crop assessments we also quantified damage to fruit, pests on fruit, and pests and natural enemies on plants using standard plant shaking protocols. Fruit was examined for stink bug and caterpillar pest damage also following UC IPM guidelines. Assessments were conducted at three distances into the crops: 10, 100, and 200 m from focal field edges, along the two transects described above. We also quantified number of fields within field type (hedgerow or control) that reached threshold levels for insecticide treatment based on UC IPM guidelines.

2.4. Stink bug control experiment

Stink bugs, primarily consperse stink bugs (*Euschistus conspersus*) are a pest of processing tomato and other fruit crops in our study region. To assess if the presence of a hedgerow affected stink bug parasitism and predation rates we used sentinel stink bug egg masses placed in field edges and into adjacent crops. In April each year, we collected consperse stink bug adults from weedy areas in our study region. Adults were put into sealed, ventilated plastic containers lined with brown paper towels and fed organic green beans and sunflower seeds *ad libitum*. Every two to three days, we removed the paper towel lining and cut out any egg masses that had been laid. Egg masses were immediately transferred to a -20°C freezer to ensure preservation, and to ensure that egg masses were not viable and therefore there was no chance of inadvertent infestation of commercial fields by out sentinel egg masses.

In early July, when stink bug egg control by natural enemy insects would be most essential for tomato crops in our region, we placed the sentinel egg masses in field edges and crops. In 2009 we placed 20 egg masses along the edge of crops and 10 egg masses at each of 10, 100, and 200 m into fields. In 2010 we placed 15 egg masses in the edge and 15 at each of the three distances into fields. In control edges we clipped egg masses to the underside of broad-leaved weeds if present, or around wire flag stakes if no broad-leaved vegetation was present. In both cases, egg masses were covered by vegetation and oriented with the egg mass towards the ground, mimicking how stink bugs lay their eggs. In hedgerow edges, egg masses were clipped with metal hairpins to the underside of native shrub leaves. In fields, egg masses were clipped to the underside of tomato leaves, at approximately 1/3 from the bottom of the plant. Egg masses had a mean (SE) of $14.8(\pm 0.17)$ eggs. At each distance, egg masses were placed approximately 10 m distant from each other, parallel to the focal field edge.

After five days, egg masses were collected and placed into individually labelled and ventilated plastic bags and kept at room temperature. Egg masses were left for one month in order to allow parasite development which results in the development of characteristic black eggs following parasitism. After one month, egg masses were assessed for parasitism or predation. Predation was counted when egg masses were either completely consumed or had caps and contents removed. Generally, predated egg masses had no intact eggs left. Parasitism was counted if egg masses were dark black and/or emergence or partial emergence of parasitoids was observed (Ehler, 2000).

2.5. Data analysis

2.5.1. Sweep samples

The mean number of pest, parasitoid, and predator arthropods were compared between edge types using separate mixed model ANOVAs with Poisson distributions, sample round as a repeated factor, and site, nested within treatment and year as

a random factor (GLIMMIX procedure, SAS). Sites that were the same between years had the same code and were not treated as independent sites between years. Within pest, predator, and parasitoid groups, we also calculated abundance of finer taxonomic groupings (Table 1) to compare differences in abundance of each group between control and hedgerow edges using the same model as above. Predator richness (using identification level in Table 1) was compared among edge types using the same model. We also calculated accumulation curves using the six sub-samples during each of the four sample rounds (for a total of 24 sub-samples per site) and calculated a jackknife estimator of predator richness (Jack1, McCune and Grace Analysis of Ecological Communities). We did not calculate diversity or evenness estimates because of the varying levels of identification among predator types.

2.5.2. Sticky card samples

Abundances of pests, predators, and parasitoids were compared between treatment types using the same model as above but with distance into field as a covariate (0, 10, 100, 200 m) and the interaction between distance and treatment as a main effect. This model also was used to compare abundances of specific pest and predator groups (Table 1). Richness and diversity of predators (identification level in Table 1) were compared between treatments. A Poisson or negative binomial distribution was used for each model.

2.5.3. Visual assessment of field pests, natural enemies, and crop damage

We compared proportion of leaves with aphids (using a binomial distribution), number of pest and beneficial insects from plant shakes, and number of fruit with pest damage using the same model as for sticky card data analyses. For both sticky card data and crop assessments, if insecticides (excluding miticide treatment which has little effect on the pest insects that we were assessing) were used on the field, data from that field was not used after the application for that season. This excluded one sample round from one control site in 2009 and one sample from each of one control and one hedgerow site in 2010.

2.5.4. Stink bug control experiment

Number of predated egg masses divided by the total number of egg masses collected was compared among distances and between treatment types using a mixed model ANOVA with a binomial distribution. Site, nested in treatment and year was a random factor. The number of parasitized eggs over the number of eggs in each egg mass (excluding predated egg masses because we could not tell if predated egg masses were, or would have been, parasitized) was compared among distances and field types with the same mixed model ANOVA as for egg mass predation. Note that we report on proportion of egg masses parasitized because this is how pest management decisions are made, however we analysed number of eggs parasitized in each egg mass over total number of eggs in that egg mass as a more precise measure.

3. Results

3.1. Edge sweep samples

Overall, the most common predators in edges (total individuals collected) were minute pirate bugs (933), spiders (829), green lacewings (108), convergent lady beetles (99), syrphid flies (94), big-eyed bugs (93), and collops beetles (86). There were no differences in total overall predator abundance from sweep samples between hedgerow and control field edges. We found no differences in abundance of any predator groups between edge types (Fig. 1a). However, richness of predators was greater in hedgerows than control edges (First order Jackknife estimator) ($F_{1,10} = 12.16, P = 0.006$) with means (SE) of 19.14 (.82) and 15.12 (.81) respectively. There was no difference in the overall number of parasitoid individuals collected in sweep samples between hedgerow and control edges (Fig. 1b), but sticky card collection was a better means of collecting these minute, flying insects.

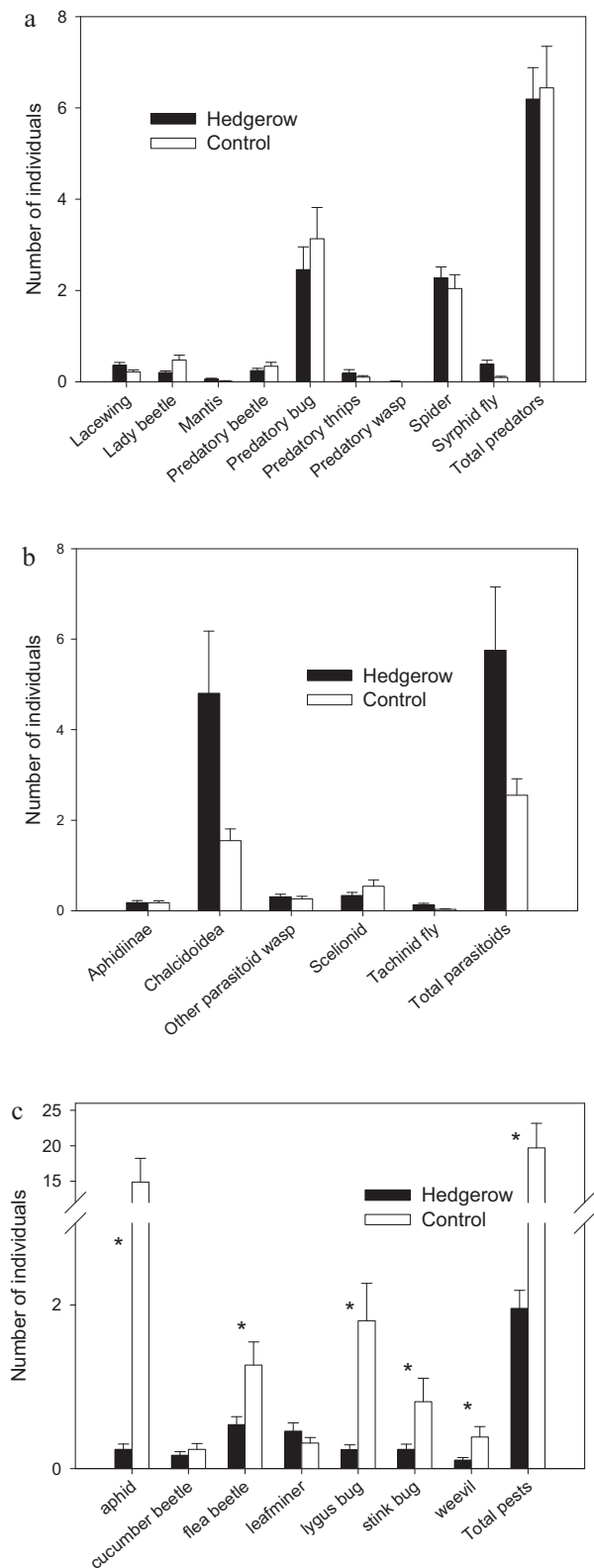


Fig. 1. Mean (+standard error) abundance of (a) predators, (b) parasitoids, and (c) pests in control and hedgerow field edges over two years per sweep net sample. Data are from four hedgerows and four control edges over two years. Stars above bars for each group indicate differences in mean abundance per sample between hedgerow and control sites ($P < 0.05$).

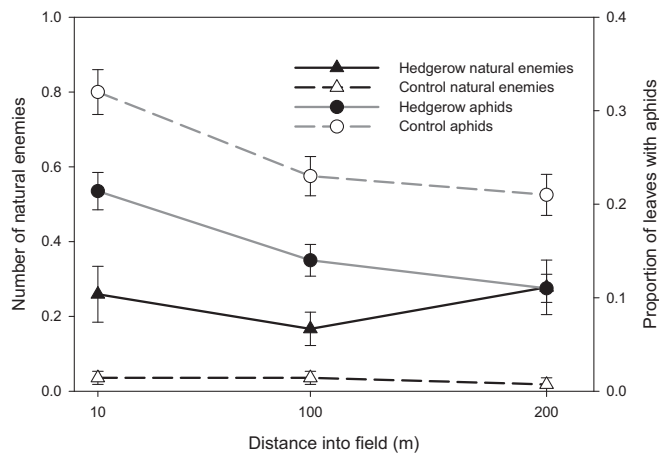


Fig. 2. Crop assessments of natural enemies (predators; triangles) per shake sample and proportion of leaves with aphids (circles) in fields with and without adjacent hedgerows. These were the only two response variables from crop IPM assessments that differed between hedgerow and control sites. Pairwise comparison at each distance showed significant differences between hedgerow and control sites at each of the three distances for both natural enemies and proportion of leaves with aphids ($P < 0.05$). All other factors including stink bug abundance and fruit damage by pests were non-significant.

The five most abundant pest groups (total individuals collected) were aphids (3018), lygus bugs (401), flea beetles (397), stink bugs (208), and leafminers (160). There were significantly more pest insects in control than in hedgerow edges in sweep samples ($F_{1,10} = 14.71$, $P = 0.003$; Fig. 1c). All pest groups, except leafminers, were significantly more abundant in control edges than in the native hedgerow vegetation ($P < 0.05$; Fig. 1c). Sweep sample data showed a larger beneficial arthropod (predators + parasitoids) to total arthropod ratio at hedgerow than control sites (0.81 ± 0.02 and 0.52 ± 0.03 respectively; $F_{1,10} = 18.47$, $P = 0.002$).

3.2. Sticky card samples

There were significantly more parasitoids in the hedgerow than control sites ($F_{1,10} = 6.75$, $P = 0.026$) and a decrease with distance into fields at both site types ($F_{1,630} = 100.7$, $P < 0.0001$). Pairwise comparison showed significantly more parasitoids at all distances up to and including 100 m into fields (critical P -value Bonferroni-adjusted based on number of pre-planned comparisons). There was no effect of site treatment on predator number, but significant decrease in predator abundance with distance into fields ($F_{1,632} = 5.67$, $P = 0.02$), however, sticky cards do not sample most predatory insects very well and we did not examine abundance of predator groups due to low numbers captured by this method. Similarly there was no effect of treatment on predator richness or diversity, but a significant decrease of both with distance into fields ($P < 0.05$).

Overall, there was a significant decrease in pests into fields ($F_{1,630} = 29.6$, $P < 0.0001$) and less pests in hedgerow than control sites ($F_{1,10} = 5.2$, $P = 0.046$). Pairwise comparisons of means showed that there were fewer pests on sticky cards at 0 m ($P = 0.04$) and 10 m ($P = 0.048$) at hedgerow sites than control sites, and no differences at 100 and 200 m into fields. The most abundant pest group on sticky cards were leafminers (total = 4778) followed by aphids (total = 3401). There was no difference in leafminer abundance between the two field types. Aphids (mainly *M. euphorbiae*) were substantially more abundant at control than hedgerow sites ($F_{1,10} = 25.22$, $P = 0.0005$), however, the difference was only significant at 0 and 10 m and there was no difference in aphid abundance on sticky cards at 100 or 200 m into fields.

3.3. Visual assessment of field pests, natural enemies, and crop damage

A greater proportion of leaves had aphids on them in control sites than hedgerow sites ($F_{1,10} = 6.55$, $P = 0.03$; Fig. 2) at all distances into fields ($P < 0.05$), with the proportion of tomato leaves with aphids declining with distance into fields at both site types ($F_{2,886} = 29.23$, $P < 0.0001$).

Fields that were treated with insecticides may have been treated because pest numbers reached levels that indicated treatment based on UC IPM guidelines, or fields may not have reached threshold levels for treatment but were treated based on judgement by the grower and pest advisor. Therefore, to compare number of fields that warranted pest control based on UC IPM guidelines, we again excluded fields that were treated prior to our assessments. In 2009, no fields reached the threshold recommended level for treatment of aphids during our assessments (50% or greater of leaves having aphids) although one control field was treated for aphids between our second and third assessment. In 2010, three control fields and one

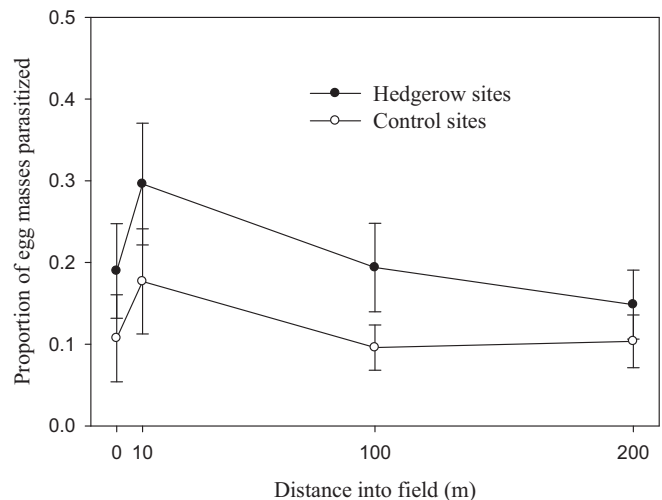


Fig. 3. Mean (\pm standard error) proportion of sentinel parasitized stink bug egg masses over two years, 2009–2010. Analysis was done on number of eggs in each egg mass that was parasitized (mixed model ANOVA with binomial distribution) and showed greater parasitism at hedgerow sites ($P < 0.05$) at 0, 10, and 100 m.

hedgerow field reached the threshold for aphid treatment. The hedgerow field subsequently was treated and one of the control fields was treated for aphids after our assessments. Therefore, 3/8 of control and 1/8 of hedgerow fields reached the threshold for aphid treatment during our assessments, and 4/8 of control and 1/8 of hedgerow fields were actually treated for aphids. The only hedgerow field over the two years of the study that reached the threshold level for aphid treatment also had a greater understory of weeds with aphids than the other hedgerow sites.

There were more natural enemy insects, mostly made up of the native lady beetle, *Hippodamia convergens*, at hedgerow than control sites ($F_{1,10} = 5.77$, $P = 0.037$; Fig. 2) with no decline in natural enemies up to 200 m into fields. All other pests including stink bugs, indicators of pests, and fruit damage were found rarely, below recommended treatment levels, and showed no differences among treatment types.

3.4. Stink bug parasitism experiment

Of the 871 egg masses recovered (394 of 400 in 2009, and 477 of 480 in 2010), 82 were predated and 127 were parasitized. There was no difference in predation between site types, but there was a highly significant effect of distance ($F_{3,45} = 18.0$, $P < 0.0001$) with a predation rate of 20% in edges and between 1 and 4% in fields. Most predation seemed to be from small mammals, possibly mice or other small rodents, as evidenced by complete removal of egg masses and chew marks on the paper towel.

Overall parasitism was 20% and 18% in 2009 and 2010 respectively. Egg mass parasitism was significantly greater at hedgerow (20%) than control sites (12%). Analyses of variance of number of eggs parasitized showed a significant distance by treatment interaction ($P < 0.0001$) and we therefore report on planned comparisons between hedgerow and control parasitism at each of the four distances. Parasitism was greater at hedgerow sites than control sites at 0, 10, and 100 m ($P = 0.002$, $P = 0.02$, $P < 0.0001$ respectively; Fig. 3).

4. Discussion

We found that small-scale restoration in intensive agricultural landscapes can enhance some natural enemies, both in edges and in adjacent crops, while decreasing pests in edges and adjacent crops. Parasitoids were more abundant at hedgerow than control edges, possibly due to the greater floral resources in the hedgerows than control edges (Morandin and Kremen, 2013). Restored hedgerows in our study were planted with flowering shrubs that provide continuous bloom over the growing season and many parasitoid wasps rely on non-host food resources, mainly nectar (Landis et al., 2000). In addition, having non-crop floral resources has been shown to increase longevity and fecundity of parasitoids (Winkler et al., 2006; Geneau et al., 2012).

The relative abundance of parasitoids at distances from restored areas compared to abundances at distances from control edges can indicate whether hedgerows were acting as net exporters or net

concentrators of populations (Morandin and Kremen, 2013). For example, if there was a lower abundance of parasitoids in crops adjacent to hedgerows than in crops adjacent to control edges, this would suggest that hedgerows were concentrating existing populations, attracting parasitoids away from crop areas more so than weedy field edges. Because we did not see that pattern but conversely saw greater numbers of parasitoids in crops adjacent to hedgerow than control edges, our data suggest that hedgerows were exporting parasitoids to adjacent fields. Greater parasitoid abundance in edges and adjacent fields could result in greater parasitism of crop pests. However, some parasitoids sampled may be hyper-parasitoids, targeting other parasitoids rather than pest insects.

Contrary to our expectations, we did not find greater predator abundance in hedgerows compared to control edges in sweep samples or on sticky cards. While many predatory arthropods also benefit from floral resources (Bianchi et al., 2006), they are possibly less dependent on them than parasitoids, many of which require nectar as an energy source. Predatory insects in our study likely benefited from the greater abundance of pest insects in the control, weedy edges. In hedgerow edges predators likely were supported in equal numbers as control sites by a combination of enhanced floral resources, enhanced overwintering habitat, and non-pest prey.

Although equivalent numbers of predatory arthropods were found at both edge types, hedgerows had greater predatory arthropod richness than weedy edges. While it is relatively clear that greater natural enemy abundance is beneficial to pest control, it is less clear as to whether greater natural enemy diversity is beneficial to biocontrol (Letourneau and Bothwell, 2008). Theory and some evidence suggests that more complex communities, with greater predator diversity, result in less effective pest control because of intraguild predation (e.g. Finke and Denno, 2004). Yet, other evidence suggests that more diverse communities of natural enemies may be more effective at suppressing pest populations than less diverse communities because they are more likely to contain predators or parasitoids that are effective regulators of a variety of pest species (Myers et al., 1989), can better adjust to changing climate (Tscharntke et al., 2007), or may have synergistic effects (Losey and Denno, 1998; Straub and Snyder, 2008). Our data indicate that greater predator richness, at minimum, did not weaken pest control services and may have enhanced them as evidenced from lower pest abundances in hedgerows (with higher predator diversity) than pest abundance in control sites (with lower predator diversity).

In addition to greater parasitoid abundance and predator richness, hedgerows in our study had lower abundances of economically important pest insects in both hedgerow edges and partially into adjacent crops compared to control sites, possibly due to a number of interacting factors. First, some weedy vegetation common in unmanaged edges, such as *Brassica* spp, and *Malva neglecta*, harbor common crop pests including aphids and stink bugs (personal observation), while pest insects are not supported on most native hedgerow plant species (this study and Morandin et al., 2011). Second, parasitoid Hymenoptera were more abundant in edges and fields (up to at least 100 m) at hedgerow than control sites and could have contributed to keeping pest numbers at lower levels in hedgerow than control sites. Third, predator numbers were similar between hedgerow and control sites, with fewer pests at hedgerow sites, making the predator:pest ratio greater at hedgerow sites. Additionally, tomato plant shakes showed greater abundances of the native predator, convergent lady beetle, in hedgerow than control fields. Finally, the greater richness of predator types in hedgerow than control edges could have provided better pest control in edges and adjacent crops than the less diverse communities in control edges.

Assessments of pests on tomato leaves showed more aphids in fields adjacent to weedy field edges than adjacent to hedgerows. This difference extended up to 200 m, the maximum extent of our observations from edges. Only a small proportion of aphids have wings, and thus most are not captured readily on sticky cards; therefore, direct observations on leaves was a more accurate reflection of pest pressure as described in UC IPM guidelines. The lower number of aphids in crops adjacent to hedgerows could have resulted from the smaller source population in hedgerows than control edges. The greater natural enemy abundance (mainly native lady beetles which prey on aphids) and greater parasitoid abundance (some of which use aphids as hosts) up to 100 m into hedgerow fields than control fields could also explain the lower aphid abundance in fields with adjacent hedgerows. Even with treated fields removed from analyses (mainly control fields that would have had high aphid abundance if not treated), we still found significantly fewer pests, greater natural enemy abundance, and a greater ratio of beneficial to pest insects in crops adjacent to hedgerows.

Many of the fields with rotational crops in our study were approximately 400 m × 400 m (16 ha). Therefore, 200 m is the field middle and the maximum extent from edges. For aphids, the major pest found during the years of our study, and natural enemies (from visual observations on leaves and plant shakes), the benefit of hedgerows extended 200 m, into field centers. However, in the case of parasitoid abundance and parasitism of stink bug egg masses, we found enhanced populations and parasitism up to only 100 m from hedgerows, with no difference between hedgerow and control fields at 200 m. Similarly, Long et al. (1998) using marking experiments found that beneficial insects moved from perennial shrub hedgerows into adjacent crops, generally in declining abundance, up to 80 m from edges (the extent of most of their collections). This highlights the need to integrate conservation areas *within* large fields or to separate larger fields into smaller plots in order to obtain maximal benefit from parasitoids and predators with more restricted movement.

While we found evidence that hedgerow restoration resulted in some pest populations being kept below economic thresholds for treatment, the stink bug egg mass parasitism experiment showed less compelling evidence that hedgerows could reduce pests below economic threshold levels requiring insecticide treatment. The significantly greater parasitism of eggs up to 100 m into fields with hedgerows, still only had parasitism rates of 10–20%, not sufficient to keep stink bug populations below economic thresholds for treatment in years where stink bugs are abundant (Ehler, 2000). However, our experiment necessitated collecting and freezing egg masses to 1. get sufficient numbers and, 2. so that there was no chance that egg masses were viable and could hatch in fields. Frozen egg masses begin to rot or become desiccated within a few days of thawing, and therefore are probably only attractive to parasitoids for a few days. Fresh egg masses on the other hand, in fields for the entire duration of egg life (approximately 4 wk depending on ambient temperature) are exposed to potential parasitism for at least the first couple of weeks of gestation and thus the 10–20% level of parasitism we found during only 5 d using frozen egg masses may be a low estimate.

Differences in crop damage and/or yield arguably are the best way to assess if biocontrol is enhanced from restoration practices. However, it is difficult to get meaningful data on damage or yield in commercial fields due to differences in farm characteristics, management practices, and crop varieties. Growers manage crops in order to minimize crop damage and generally treat fields with insecticides when arthropods reach threshold levels. Therefore, not surprisingly, pest damage was uniformly low across all fields and years in our study. However, 4 of 8 control vs 1 of 8 hedgerow fields, either reached treatment thresholds for aphids and/or were

treated for aphids. This could translate into economic returns from hedgerow restoration resulting from growers requiring fewer pesticide applications.

Acknowledgements

We thank J. Muller, H. Wallis, and S. Kaiser for laboratory and field management, data collection, and insect identification. We thank the growers and land owners that allowed us access to their fields. L. Ehler helped with stink bug rearing, data collection, and insect identification. The research was funded by an NSERC Postdoctoral Fellowship to L.A.M., a Conservation Innovation Grant to C.K. and the Xerces Society, a UC Davis Hatch fund to L. Ehler, and a National Geographic Society Research and Exploration grant to L.A.M. and C.K.

References

- Bianchi, F., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Lond. Biol.* 273, 1715–1727.
- Bugg, R.L., Anderson, J.H., Thomsen, C.D., Chandler, J., 1998. Farmscaping in California: hedgerows roadside plantings and wild plants for bio-intensive pest management. In: Pickett, C.H., Bugg, R.L. (Eds.), *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests*. University of California Press, Berkeley, CA, pp. 339–374.
- Chaplin-Kramer, R., Kremen, C., 2012. Pest control experiments show benefits of complexity at landscape and local scales. *Ecol. Appl.* 22, 1936–1948.
- 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. *Ecol. Lett.* 14, 922–932.
- Ehler, L.E., 2000. *Farmscape Ecology of Stink Bugs in Northern California*. Entomological Society of America, Lanham, Maryland.
- ESRI, 2009. ArcMap ESRI, Redlands, California.
- Finke, D.L., Denno, R.F., 2004. Predator diversity dampens trophic cascades. *Nature* 429, 407–410.
- Geneau, C.E., Wackers, F.L., Luka, H., Daniel, C., Balmer, O., 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic Appl. Ecol.* 13, 85–93.
- Griffiths, G.J.K., Holland, J.M., Bailey, A., Thomas, M.B., 2008. Efficacy and economics of shelter habitats for conservation biological control. *Biol. Control* 45, 200–209.
- Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecol. Soc.* 17.
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175–201.
- Letourneau, D.K., Armbrrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutierrez, C., Lopez, S.D., Mejia, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21, 9–21.
- Letourneau, D.K., Bothwell, S.G., 2008. Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Front. Ecol. Environ.* 6, 430–438.
- Long, F.R., Corbett, A., Lamb, C., Reberg-Horton, C., Chandler, J., Stimmann, M., 1998. Beneficial insects move from flowering plants to nearby crops. *Calif. Agric.* 52, 23–26.
- Losey, J.E., Denno, R.F., 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79, 2143–2152.
- Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci. U.S.A.* 108, 11500–11505.
- Morandin, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.* 23, 829–839.
- Morandin, L.M., Long, R.F., Pease, C., Kremen, C., 2011. Hedgerows enhance beneficial insects on farms in California's Central Valley. *Calif. Agric.* 65, 197–201.
- Myers, J.H., Higgins, C., Kovacs, E., 1989. How many insect species are necessary for the biological control of insects? *Environ. Entomol.* 18, 541–547.
- Stamps, W.T., Dailey, T.V., Gruenhagen, N.M., Linit, M.J., 2008. Soybean yield and resource conservation field borders. *Agric. Ecosyst. Environ.* 124, 142–146.
- Straub, C.S., Snyder, W.E., 2008. Increasing enemy biodiversity strengthens herbivore suppression on two plant species. *Ecology* 89, 1605–1615.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309.
- Winkler, K., Wackers, F., Bukovinszki-Kiss, G., van Lenteren, J., 2006. Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions. *Basic Appl. Ecol.* 7, 133–140.