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Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields

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Abstract

California's central coast differs from many agricultural areas in the U.S., which feature large tracts of monoculture production fields and relatively simple landscapes. Known as the nation's salad bowl, and producing up to 90% of U.S. production of lettuces, broccoli and Brussels sprouts, this region is a mosaic of fresh vegetable fields, coastal meadow, chaparral shrubs, riparian and woodland habitat. We tested for relationships between the percent cover of crops, riparian and other natural landscape vegetation and the species richness of parasitic wasps and flies foraging in crops, such as broccoli, kale and cauliflower, and interpreted our results with respect to the decrease in natural habitat and increase in cropland cover prompted by a local microbial contamination event in 2006. Our key results are that: (1) as cropland cover in the landscape increased, fewer species of parasitoids were captured in the crop field, (2) parasitoid richness overall was positively associated with the amount of riparian and other natural vegetation in the surrounding 500m, (3) different groups of parasitoids were associated with unique types of natural vegetation, and (4) parasitism rates of sentinel cabbage aphid and cabbage looper pests were correlated with landscape vegetation features according to which parasitoids caused the mortality. Although individual species of parasitoids may thrive in landscapes that are predominantly short season crops, the robust associations found in this study across specialist and generalist parasitoids and different taxa (tachinid flies, ichneumon wasps, braconid wasps) shows that recent food safety practices targeting removal of natural vegetation around vegetable fields in an attempt to eliminate wildlife may harm natural enemy communities and reduce ecosystem services. We argue that enhancing biological diversity is a key goal for transforming agroecosystems for future productivity, sustainability and public health.

Introduction

Ecosystem services, though vital for the future of U.S. agricultural production and profitability (Daily et al., 1997; Losey and Vaughan, 2006), are severely threatened by agricultural intensification (Butler et al., 2007; Power, 2010). Pollinator declines, persistent crop losses from pests, increases in crop and water contamination, and variable climate effects on projected food production have prompted major research and policy initiatives in the U.S. and Europe targeting sustainable crop production and biodiversity conservation (Balvanera et al., 2001; Bianchi et al., 2006; Tai et al., 2014). Introducing crop diversification schemes and maintaining or restoring vegetational diversity in agricultural landscapes are key elements for transformation in agricultural

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practices designed to mitigate negative trends set in place through intensification (Letourneau et al., 2011; Nicholls and Altieri, 2013; Andersson et al., 2014). Multiple benefits accrue from diversification and restorative practices; maximizing biological control of insect pests in agriculture requires stable habitat for beneficial insects and restricted use of insecticides, both of which in turn contribute to improved water quality, increased biodiversity, and elevated carbon sequestration (Nicholls and Altieri, 2007; Landis et al., 2008; Zhang et al., 2010; Meehan et al., 2011; Asbjornsen et al., 2014).

Habitat stability for natural enemies of insect pests increases biological control services in perennial crops (Southwood, 1977; Geiger et al., 2009), such as orchards and agroforestry systems (Alam et al., 2014), yet annual and short-cycle cropping systems remain particularly vulnerable to insect pest outbreaks (Wiedenmann and Smith, 1997; Letourneau and Altieri, 1999). Habitat disturbance (soil fumigation, tillage, bare fallow, rapid harvests) disrupts community development (Landis and Menalled, 1998; Letourneau, 1998), thus forcing beneficial insects into patterns of 'cyclic colonization' from refuge habitats (Wissinger, 1997). If these refugia are unavailable within a suitable distance from emerging pest irruptions, the abundance and diversity of beneficial insects is reduced along with the pest control services they provide in crop fields (Barbosa and Benrey, 1998). With annual vegetables being among the most highly disturbed (more frequent tillage and harvests than corn, wheat and soy) and pesticide-intensive production systems, potential benefits of enhancing parasitoid diversity, biological control services and reduced pesticide dependence are considerable. Clearly, the conservation, restoration, or establishment of on-farm or surrounding vegetation is a promising area of research and policy development (Ehler, 1998; Thies et al., 2003; Landis et al., 2005; Chaplin-Kramer et al., 2011; Thies et al., 2011).

Although the Monterey Bay region has not experienced the levels of intensification seen with crops in California's central valley or in the corn belt of the Mid-West, there have been pressures on growers in recent years to create 'sterile farming conditions' as a way to reduce the probability of pre-harvest microbial contamination in fresh produce. We call attention here to the Food Safety Modernization Act of 2014 and other policies enacted in response to the 2006 disease outbreak caused by enterohemorrhagic *Escherichia coli* (Migula) Castellani and Chalmers O157-H7 in California spinach. One measure that was implemented on the Central Coast region was the removal of non-crop vegetation around agricultural fields in an attempt to reduce wildlife movement into leafy greens production areas. Sutherland et al. (2012) recognized these measures as among the top emerging issues for biodiversity conservation. Furthermore, loss of associated ecosystem services is of concern if non-crop vegetation surrounding fields increases natural enemies of pests and other beneficial insects in ephemeral crops (Marino et al., 2006; Tschardt et al., 2008; Chaplin-Kramer et al., 2011). We reported previously a positive association between non-crop habitat in farm landscapes and parasitoid fly diversity in organic crop fields (Letourneau et al., 2012).

Here, we examine more broadly the associations between non-crop vegetation surrounding central coast vegetable fields, parasitoid diversity and parasitism rates of pest insects. We combined specific vegetation types into categories that match those used by Karp et al. (2015) in their study of microbial contamination and landscape vegetation composition. Given their documented decrease in non-crop vegetation and increase in cropland after the 2006 *E. coli* contamination event, we asked the following specific questions about parasitoids we captured in fields in 2005: (1) Was there a relationship between the number of species of parasitoids visiting vegetable crops and the amount of cropland versus non-crop vegetation surrounding those fields? (2) If so, is there evidence that riparian habitat or other natural vegetation around farm fields increased the diversity of different types of parasitoids in farm fields? (3) Were the habitats around the farms associated with parasitoid diversity for different kinds of insect herbivore hosts? (4) Was the relative amount of insect pest mortality due to parasitoids associated with landscape vegetation characteristics? Our results complement the study by Karp et al. (2015) of non-crop vegetation removal for food safety by examining the implications of such interventions for beneficial insects and pest control services.

Methods

Study sites

Parasitoid fly and wasp richness and parasitism levels were measured in California certified organic crop fields located on coastal terraces and valleys within a 1,500 Km² area near the Monterey Bay. Monterey, Santa Cruz, and San Benito counties are highly productive agriculturally and have a disproportionately high number of organic growers farming ~40% of the acreage in vegetable production (Nicoletti, 2014). The region also supports a high diversity of native plant species in wetlands, chaparral, oak woodlands and coastal prairies (Press et al., 1996). Our sample fields represented land under production by 25 growers listed in the directory of California Certified Organic Farmers as producers of cole crops and/or lettuce. Crop fields had vegetable rotations, including up to 10 varieties of broccoli, cabbage, kale, arugula or other cole crops, lettuces, and some mixed cropping of melon, squash, cucumbers, carrots, beets, tomato and strawberry.

Fields exist within landscapes encompassing a diverse array of vegetation types and other land uses ranging from primarily homogenous cover of annual crops to primarily forest trees and native shrubs (Fig. 1). Using color-infrared and black-and-white digital aerial orthophotos (courtesy of the Association of Monterey Bay Area Governments) in a GIS, ranging from six-inch to two-foot resolution, we manually digitized, characterized, and then measured the percent cover of each type of vegetation within a 1500m radius circle around the center (geometric mean center from crop field perimeters) of each of 35 fields. We also calculated percentage cover for the areas within the inner 500m radius (Fig. 1). Each polygon in the GIS was designated by hand (trained digital scanning software was not used) with one of nine land-use (e.g., annual or perennial cropland, paved or gravel roads, industrial and residential areas) or forty-one vegetation classes, determined ad hoc, based on our ability to characterize them by interpreting hue/tone, texture, and shape (e.g., the vegetation class 'conifers' was made up of genera such as *Sequoia*, *Pinus*, and *Pseudotsuga*, which were not reliably distinguishable from each other). Groundtruthing for these categorizations of vegetation, which comprised field visit checks of 300 stratified-randomly selected points within the 34 digitized landscapes, showed a >89% accuracy rate (see Bothwell, 2012). In this paper, we analyzed only the vegetation within a 500m radius of the field center to minimize the number of comparisons. This scale has been used in previous studies to test for effects of landscape elements on the abundance, composition and diversity of insects

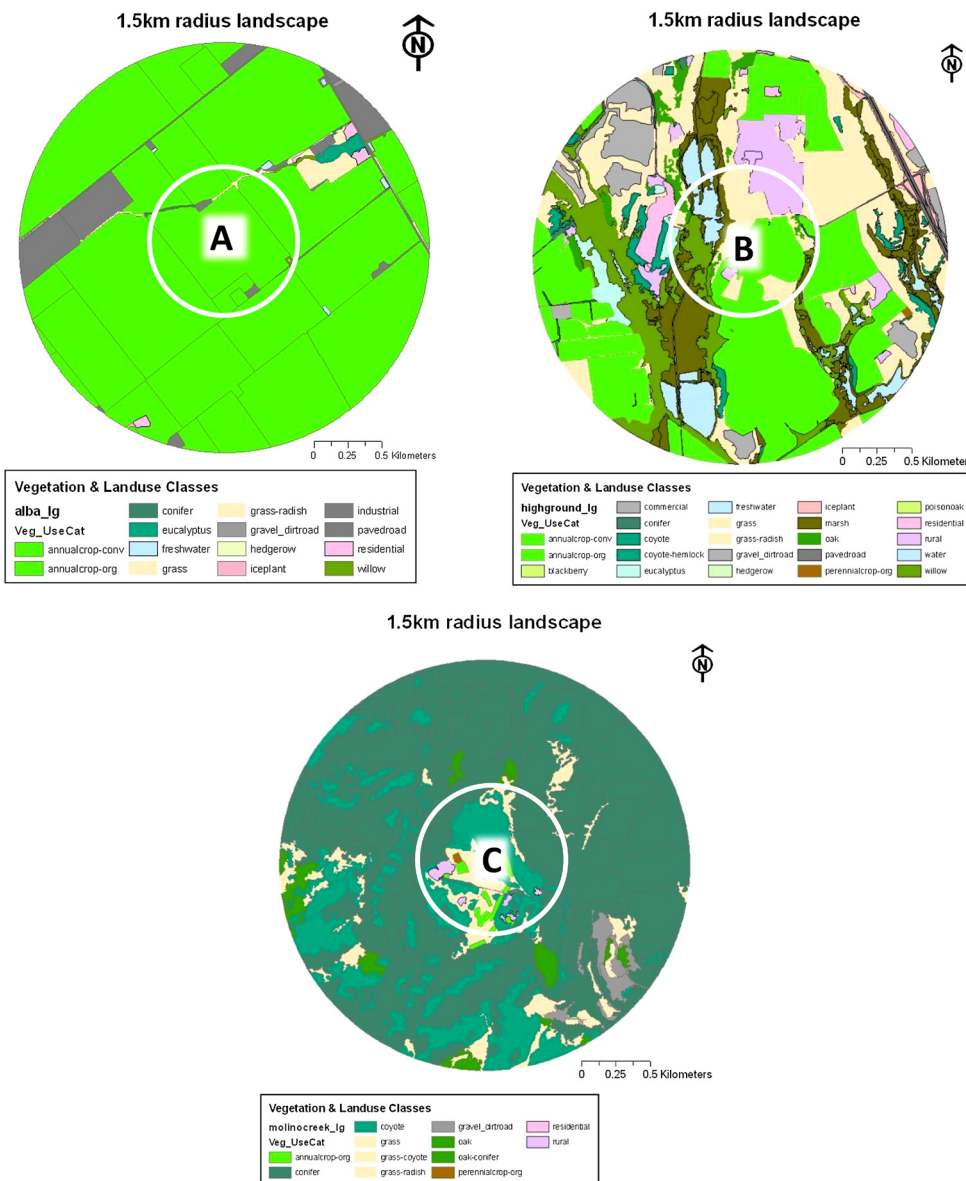


Figure 1

Three examples of landscapes surrounding a central field sampled for parasitoid richness and abundance.

Vegetation types are shown for both a 1500m and 500m radius around farm fields with contrasting landscape conditions such as: A) high coverage of annual cropland (bright green), B) intermediate annual cropland (bright green) with high cover of coastal prairie (peach) along with a variety of other vegetation types such as riparian/willow and marsh habitat (muddy greens), and C) low coverage of annual cropland with high conifer and coyote brush cover (dark greens) with some grassland and blackberry cover.

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visiting crop fields, for example by Letourneau and Goldstein (2001) for herbivores, predators and parasitoids; Thies et al. (2003) for herbivores and parasitoids; and Kremen et al. (2004) for native bees. Most parasitoids can disperse across several kilometers (e.g., Munro, 1998), and trivial movement distances are likely to cover hundreds of meters and vary among species in such large and diverse families (Brodmann et al., 1997; Roth et al., 2006; Rader et al., 2011). Thus, landscape characteristics within 0.5 km may be the most relevant scale for frequented refugia, but both the 500m and 1500m scales quantified in our vegetation analysis are likely within the potential dispersal range of many of these parasitoids.

We described vegetative cover by combining plant taxa and categories into three habitat types based on Karp et al. (2015): cropland (including annual crops, vineyards, orchards, cane berries), riparian (*Salix*, *Alnus*, and *Acer*) and other natural vegetation (such as trees in the genera *Umbellularia*, *Quercus*, *Lithocarpus*, *Acer* and conifers, shrubs like *Baccharis*, *Toyon*, *Salvia*, *Artemisia* and other chaparral genera, *Manzanita*, *Rubus*, and native shrub hedgerows, and annual forbs and grasses within coastal prairies). To be consistent with their habitat designations, exotic trees (*Eucalyptus* and *Acacia*) were not included in any of these categories. We tested for associations with specific non-crop plants that were prominent in the landscapes by combining or selecting from the original 41 types of vegetation, and then using a principal components analysis (PCA), which further reduces the number of variables, but retains the character of the vegetation. Vegetation mixes that we combined within the PCA (Table 1) were denoted by dominant taxa in order of their prominence, such as oak-conifer, considering all taxa with greater than 10 percent coverage within the polygon; this yielded several 3-taxa vegetation classes, combined in our analyses according to the dominant species. For example, *Toyon-Artemisia-Baccharis* mixtures were counted as *Toyon*.

Insect sampling, identification, and host range determinations

Flying insects were collected in Malaise traps (BioQuip model 2875AG, 1.2 m wide x 2.13 m tall, with forest green netting) placed for 48 hours in the center of each of the 35 crop fields in July and September 2005 and May 2006. Parasitoid wasps and flies were extracted from the samples and identified to subfamily and species (Tachinidae) or subfamily and morphospecies (Ichneumonidae and Braconidae). Tachinidae were identified to species with the aid of published keys (e.g., Wood, 1987) and by direct comparison to reliably identified specimens in the Canadian National Collection of Insects Ottawa, Ontario. Morphospecies determinations were necessary because some groups require revision, well-illustrated keys are not available for some groups, and because authoritatively identified specimens were often not available for comparison. We required accurate species delimitation but for the analyses we did not need the identities of the species that were delimited. For several specimens in poor condition, designations were inferred from the most likely taxon to which the species belonged or they were excluded from the analysis.

Each individual parasitoid captured in Malaise traps was categorized as a specialist on Lepidoptera, Coleoptera, Diptera, Aphididae or other orders or as a generalist, with hosts in >1 order, based on host records for its genus or species (Tachinidae), or for its genus or subfamily (Braconidae), or by subfamily

Table 1. Results of principal component analysis (PCA) showing the amount of variation explained by each of the first six principal components (total = 80%) and their eigenvector loadings^a for vegetation types present in at least 15% of the landscapes within 500m of the center of sampled crop field

Plant type ^b	PC1 (20%)	PC2 (16%)	PC3 (15%)	PC4 (11%)	PC5 (10%)	PC6 (8%)
Willow	-0.0377	0.6679	-0.0555	0.2386	-0.0590	0.1418
Alder	0.4006	0.3137	0.2103	-0.0710	-0.1215	-0.1952
Maple	0.4610	-0.0151	0.0840	-0.0566	0.3902	0.5109
Grasses	-0.3140	0.1455	0.4480	0.0398	-0.0876	0.1276
Marsh	0.0605	0.5795	-0.2283	-0.2618	-0.2764	0.0788
Sage	-0.2225	-0.0374	0.4280	-0.3862	-0.1437	0.3228
Blackberry	-0.2493	0.1414	0.4247	-0.0446	0.2714	0.1825
Coyote	0.1618	-0.0058	0.4902	0.0272	-0.2089	-0.5834
Oak	-0.0343	-0.1017	0.0968	0.7729	-0.3872	0.2941
Conifers	0.5828	-0.0070	0.2793	0.1411	0.0919	0.0724
Poison Oak	-0.2112	0.2576	0.0390	0.3091	0.6702	-0.2978

^a With large loadings in bold font.

^b Categories are, in order, riparian species: willows (*Salix* spp.), alders (*Alnus* spp.), and maples (*Acer* spp.), and other natural vegetation: grassland/coastal prairie, marshland (freshwater and brackish), sagebrush (*Artemisia* spp.), blackberry (*Rubus* spp.), coyote brush (*Baccharis pilularis*), coast live oak (*Quercus* spp.), conifers (e.g., *Sequoia sempervirens*, *Pseudotsuga menziesii*, *Pinus radiata*), and poison oak (*Toxicodendron* spp.). Coffee berry (*Toyon* spp.), bay laurel (*Umbellularia californica*), and tanoak (*Lithocarpus densiflorus*) were found in <6 landscapes.

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(Ichneumonidae). Host taxa for ichneumonid subfamilies were assigned according to the identification guide (Wahl and Sharkey, 1993) and braconid and tachinid hosts were categorized based on the host records in Arnaud (1978), as well as more recent catalogs (Yu et al., 2012) and taxonomic literature (e.g., O'Hara, 1992, 1996, 2002). For example, lepidopteran specialists included the morphospecies within the braconid subfamilies Braconinae, Microgastrinae, Agathidinae and genus *Meteorus*, and the ichneumonid subfamilies Campopleginae, Metopiinae and Banchinae and tachinid species such as *Madremya saundersii* Williston.

Sentinel experiments

To investigate potential effects of landscape vegetation types on pest parasitism levels, we placed unparasitized aphids and moth larvae into the farm fields, using sentinel species that are ubiquitous pests of cole crops and host several species of specialist and generalist parasitoids.

Aphids: In May and August of 2006, three unparasitized adult aphids (*Brevicoryne brassicae* L., Hemiptera:Aphidae), reared in protective cages in a greenhouse, were placed on each of 5 small collard plants in 5cm × 5cm pots and allowed to establish small colonies for 48 hours in the cages. These growing colonies were exposed in the field for an additional 48 hours, and then brought back to the greenhouse and counted. The number of parasitized aphids developing mummies after five days was divided by the number of total aphids present when the plant was recovered from the field. Parasitism rates per farm were the average of the proportion parasitized per plant. This method confounds the abundance of parasitoids with the activity of parasitoids (how many aphids a single wasp parasitizes) more than taking a per-colony (per-plant) presence/absence of parasitism approach, but represents actual mortality, makes use of all of the data, and returns continuous estimates.

Moth larvae: In fall 2005, six unparasitized, 3rd instar larvae of *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) purchased from Bio-ServTM were placed on each of 10 potted collards plants. Each pot was placed into a large, water-filled tray to supply water and prevent larval escape, covered with 1cm² bird-netting to deter insectivorous birds, and set out among the crop plants, but distant enough that sentinel larvae could not disperse to crop foliage. After seven days of field exposure, collard plants were collected and all recovered larvae, usually 5th instars, were reared singly in Bio-ServTM trays on generalized lepidopteran diet and a 16:8 hour light-dark cycle. We recorded the fate of each of the 60 larvae per farm field and estimated mortality of *T. ni* due to parasitism by Tachinidae as the proportion of live pupae producing flies. This experiment was repeated in fall of 2007 with first instar larvae, which are preferred as hosts by hymenopteran parasitoids. Bird-netting may have deterred an unknown amount of parasitism, but was deemed necessary after a pilot trial sustained heavy losses of larvae in several fields coincident with farmer observations of foraging flocks of insectivorous birds. Birds, predatory insects, spiders, and other animals were responsible for much larval mortality in organic vegetable fields, as indicated by casual observations and the common disappearance of individual sentinels placed on potted plants.

Specimens reared from *T. ni* larvae were identified to species using keys and comparisons with known specimens. The reared specimen of the ichneumonid wasp *Therion californicum* (Cresson) was identified via comparison with authoritatively determined specimens of its junior synonym *Heteropelma longipes* Provancher (i.e., by C. F. Dasch as *Therion longipes*) in the Smithsonian Institution National Museum of Natural History, Washington, DC (USNM). The reared specimens of the ichneumonid wasp *Hyposoter exiguae* (Viereck) were determined via comparison with specimens in the USNM mostly determined by R. A. Cushman but also one paratype male.

Data analyses

We used Pearson's correlation coefficients with PC-SAS version 9.2 (SAS Institute, Inc., Cary, North Carolina, USA) to test for associations between parasitoids captured in July 2005 and for parasitism of sentinel pests exposed in the field and landscape parameters within 500m. We calculated species richness (S) and Jost's effective species richness (ES) for each of 35 farm fields (Jost, 2006) for all parasitoids, each family of parasitoids and host-based groupings of specialist and generalist parasitoids. Because richness was unlikely to be independent of abundance (or trap sample size) despite our equal sampling effort, the effective number of species (e^H) (MacArthur, 1965; Jost, 2006) represents the effects of landscape variables on true species diversity. Plant groups were numerous, and sometimes correlated with each another, so we examined the combined influence of frequently present plant groups as principal component axes (PC-SAS Princomp procedure). To reduce the potentially large number of comparisons, and thus the chance of Type I error, we tested basic hypotheses with three habitats (cropland, riparian and other natural), and in other cases, added the first four principal components (explaining 10% or more of the variance in plant parameters) to isolate which specific plant groups within non-crop habitats were most strongly associating with parasitoid-based parameters. None of the habitats, indices, or principal components are the same as reported in a previous analysis of tachinid parasitism rates of sentinel moth larvae and cover of annual crops, semi-wild perennials and annuals in landscapes (Letourneau et al., 2012).

Results

We captured a total of 6,215 individual parasitoids in Malaise traps, with 5,440 (\bar{X} =52 individuals/sample/field) of these individuals identified as Ichneumonidae, Braconidae or Tachinidae. These three key families yielded 3,258 individuals captured in July 2005, 889 in September 2005 and 1,293 in May 2006. These 5,440 individuals comprised 241 species/morphospecies. The additional 775 wasps in our samples belonged to other families such as Encyrtidae and Chalcididae, and represented an additional 0–24 morphospecies per sample. Although the vast majority of these parasitoids use herbivorous insects as hosts, some of the ichneumonid and braconid morphospecies were likely to be hyperparasitoids or attack predacious insects, and one or more chalcidoid morphospecies may have been gall wasps, feeding on plants.

The cover of cropland within 500m of the field center (n=35 fields) varied from 1 to 97%; riparian vegetation varied from 1–25%; and other natural vegetation varied from 0–73%. Forest, shrub and grassland cover within 500m ranged from 0.6–76%, 0–43% and 0.4–58%, respectively; and the number of semi-wild vegetation types present (vegetation richness) varied from 0 to 13 (1–14 for 1500m scale) (Fig. 1). The first six principal components explained 80% of the variation in landscape cover within 500m of the sampled fields (Table 1). The first axis (PC1) has large positive loadings for conifers, alder and maple trees and has a large negative loading associated with grassland cover (Table 1). PC 2 has high positive loadings for riparian and marsh vegetation and may indicate habitats that remain mesic in summer and fall. PC3, with high, positive eigenvalues for grasses and shrubs indicates more xeric chaparral and meadow vegetation. PC4 is strongly positively associated with oak woodlands. Subsequent PCA axes are less easily interpreted, and individually contribute little to explaining the overall variance.

Associations between parasitoid species richness or diversity and landscape vegetation

Parasitoid species richness overall was negatively associated with the amount of cropland cover within 500m of crop fields (i.e., total of braconids, ichneumonids and tachinids captured, Fig. 2A), which supports our hypothesized negative influence of landscape-level intensification (widespread conversion of semi-wild vegetation to cropland, thus lower complexity and greater disturbance) on natural enemy communities. Furthermore, both riparian and other natural vegetation was significantly and positively associated with parasitoid species richness (total of ichneumonids, braconids and tachinids, Fig. 2B, C), supporting our concern about negative effects of non-crop vegetation eradication around crop fields for biodiversity. The negative association between

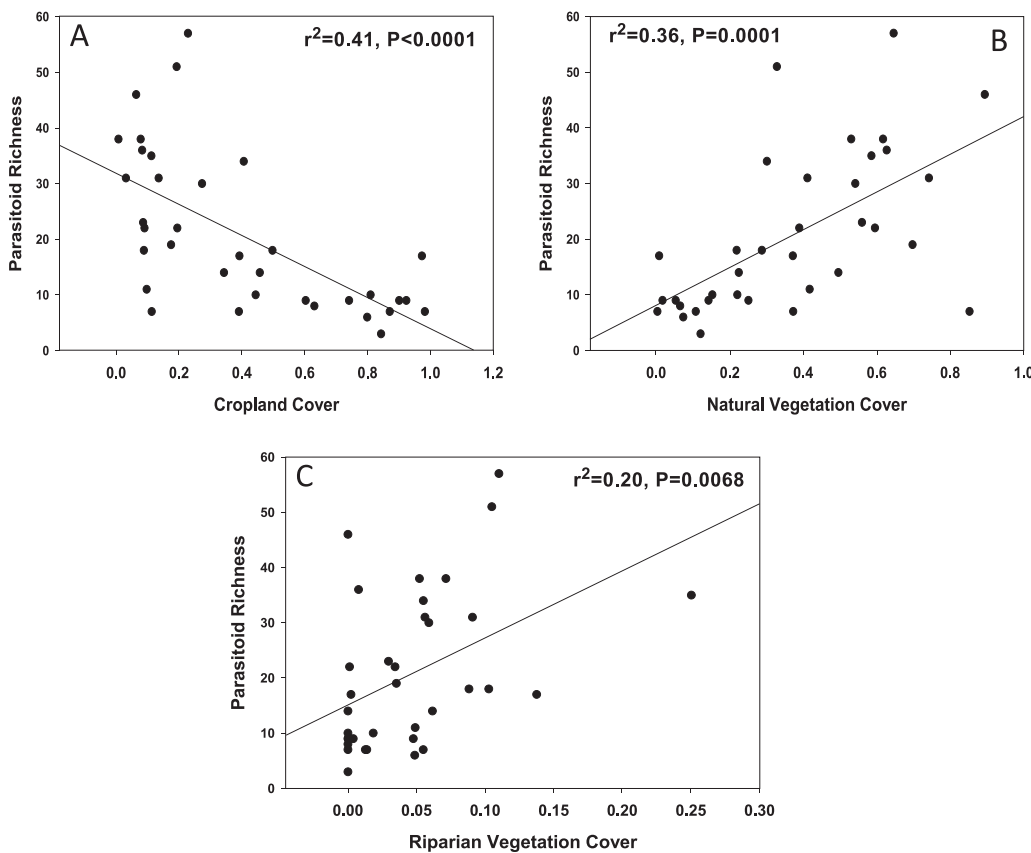


Figure 2

Associations between parasitoid species richness and landscape cover within 500m of 35 organic vegetable fields.

Plots showing significant correlations between the total species richness (ichneumonids+braconids+tachinids) in summer 2005 Malaise traps and the percentage cover of three vegetation types that changed in the region subsequent to the 2006 *E. coli* contamination event: cropland (A), natural habitat (excluding riparian and exotic trees) (B), and riparian habitat (C).

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Table 2. Associational patterns between the species richness (S) or effective species richness (ES) of tachinid fly parasitoids, ichneumon wasp parasitoids and braconid wasp parasitoids and the percent cover of crops, natural vegetation and riparian vegetation and the first four principal components based on plants^a

Vegetation variables & statistics	Tachinidae		Ichneumonidae		Braconidae	
	S	ES	S	ES	S	ES
% Cropland						
R	-0.5122	-0.2704	-0.5919	-0.5806	-0.6033	-0.6401
P-value	0.0017	0.1162	0.0002	0.0003	0.0001	<0.0001
% Natural						
R	0.5680	0.1614	0.3489	0.3259	0.3082	0.3402
P-value	0.0004	0.3544	0.0400	0.0561	0.0716	0.0455
% Riparian						
R	0.4127	0.4934	0.3573	0.2901	0.4643	0.4890
P-value	0.0137	0.0026	0.0351	0.0910	0.0050	0.0029
PC 1						
R	0.4445	0.1198	0.0685	0.0763	0.0254	0.0777
P-value	0.0075	0.4929	0.6958	0.6629	0.8847	0.6575
PC 2						
R	0.2293	0.3742	0.3164	0.2565	0.3511	0.3715
P-value	0.1852	0.0268	0.0641	0.1370	0.0386	0.0280
PC 3						
R	0.4903	0.2868	0.4104	0.3915	0.4536	0.4137
P-value	0.0028	0.0948	0.0143	0.0201	0.0062	0.0135
PC 4						
R	0.1691	0.0832	0.4855	0.4144	0.4667	0.5116
P-value	0.3316	0.6347	0.0031	0.0133	0.0047	0.0017

^aWith ES calculated as e^H .

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species richness and cropland cover was consistent and strong for species richness in Tachinidae, Ichneumonidae and Braconidae (Table 2), but the three families differed with respect to positive relationships among different habitats and vegetation types in the landscape. Tachinid parasitoids exhibited positive associations with natural and riparian habitat (Table 2), especially the plant groups with high loadings in PC1 (trees) and PC3 (grasses, chaparral shrubs). Tachinid fly diversity (e^H) was only associated (positively) with riparian vegetation cover and PC2, the vegetation restricted to wetlands. Ichneumonid wasp richness and diversity were negatively associated with cropland cover, and had positive or marginally positive relationships with riparian and natural vegetation (Table 2). Positive associations between natural vegetation cover and ichneumonid wasp richness and diversity appeared to be influenced by the presence of chaparral shrubs and/or grasses (PC3) and with oak woodlands (PC4). Braconids were most strongly associated with riparian habitats, with positive correlations for both richness and diversity. Additional significant positive associations with PC 2, 3 and 4, along with no relationship with PC1, suggest that the inclusion of forest vegetation as natural habitat weakened the positive effect of this variable on braconid richness and diversity (Table 2).

The number of species represented by the 3–353 parasitoids per farm that specialize on butterflies and moths (Lepidoptera) ranged from 3–26 in July 2005 48 hour samples, with diversity as much as six times higher in the most diverse sample ($e^H = 9.2$) as the least diverse sample ($e^H = 1.4$). Abundance, species richness, and diversity ranges for the other host-based groups were 0–10 individuals, 1–5 species and $e^H = 0–5$ for specialists on beetles, 0–135 individuals, 0–11 species and a range in e^H of 0–7.6 for specialists on flies, and 0–11 individuals, 0–5 species and e^H range from 0–4.6 for specialists on aphids. Generalist parasitoids ranged from 0–34 individuals, 0–16 species and e^H ranged from 0–14.7 per 48-hour trap sample. With a few exceptions, species richness and diversity patterns again supported our hypothesized negative relationship with cropland cover and positive association with natural and/or riparian habitat cover (Table 3). Typically, when trends with species richness (S) diverge from diversity (e^H) trends in terms of their relationship with surrounding vegetation, it means that the relative distribution of individuals among species was not even, because there were many rare species or a few species were dominant in terms of their abundance in the sample. A rare species in a 48-hr sample may still be an important member of the enemy community, so it is difficult to speculate about which parameter might hold more importance for biological control potential.

Table 3. Associational patterns between the species richness (S) or effective species richness (ES) of specialist parasitoids (on moths and butterflies, beetles, flies, aphids) and generalist parasitoids (that attack arthropods in more than one order) and the percent cover of crops, natural vegetation and riparian vegetation within 500 meters^a

Hosts	Stat	% Cropland		% Natural		% Riparian	
		Pearson's R	P-value	Pearson's R	P-value	Pearson's R	P-value
Lepidoptera	S	-0.5987	0.0001	0.5679	0.0004	0.4335	0.0093
	ES	-0.1594	0.3604	0.1179	0.5001	0.3395	0.0460
Coleoptera	S	-0.3473	0.0409	0.3941	0.0191	0.3061	0.0738
	ES	-0.3842	0.0227	0.4245	0.0110	0.2776	0.1064
Diptera	S	-0.5870	0.0002	0.4327	0.0094	0.4249	0.0109
	ES	-0.6254	<0.0001	0.4642	0.0050	0.3828	0.0232
Aphididae	S	-0.4561	0.0059	0.4397	0.0082	0.3070	0.0729
	ES	-0.3761	0.0260	0.3660	0.0306	0.3365	0.0481
General	S	-0.5637	0.0004	0.5719	0.0003	0.3146	0.0657
	ES	-0.5578	0.0005	0.5845	0.0002	0.3436	0.0433

^aWith ES calculated as e^H.
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Sentinel experiments

We used lepidopterans and aphids as sentinel pests, which, according to the host-based analyses shown in Table 3, should be associated with higher parasitoid richness on farms that have more land in natural and/or riparian vegetation, whether the parasitoids are specialists on those groups or generalists. Overall, parasitism of *B. brassicae* aphids as sentinel pests exposed for two days on five plants per field ranged from zero to 44%, with an average of 8.5% parasitism rate on recovered aphids in May and 8.6% parasitism in August 2006. The braconid *Diaretiella rapae* (M'Intosh) was most commonly reared from sentinel cabbage aphids. Spring parasitism of *B. brassicae* was positively correlated with natural vegetation cover (Fig. 3A, Table 4). None of the broad habitat variables was associated with percent parasitism in the August 2006 sentinel aphid trials, but parasitism rate was positively associated with PC4, which has a high positive loading for the percent cover of oak woodland (which includes stands of oak trees, mixed oak forest with bay trees, mixed oak and conifer, and oak dominated grassland).

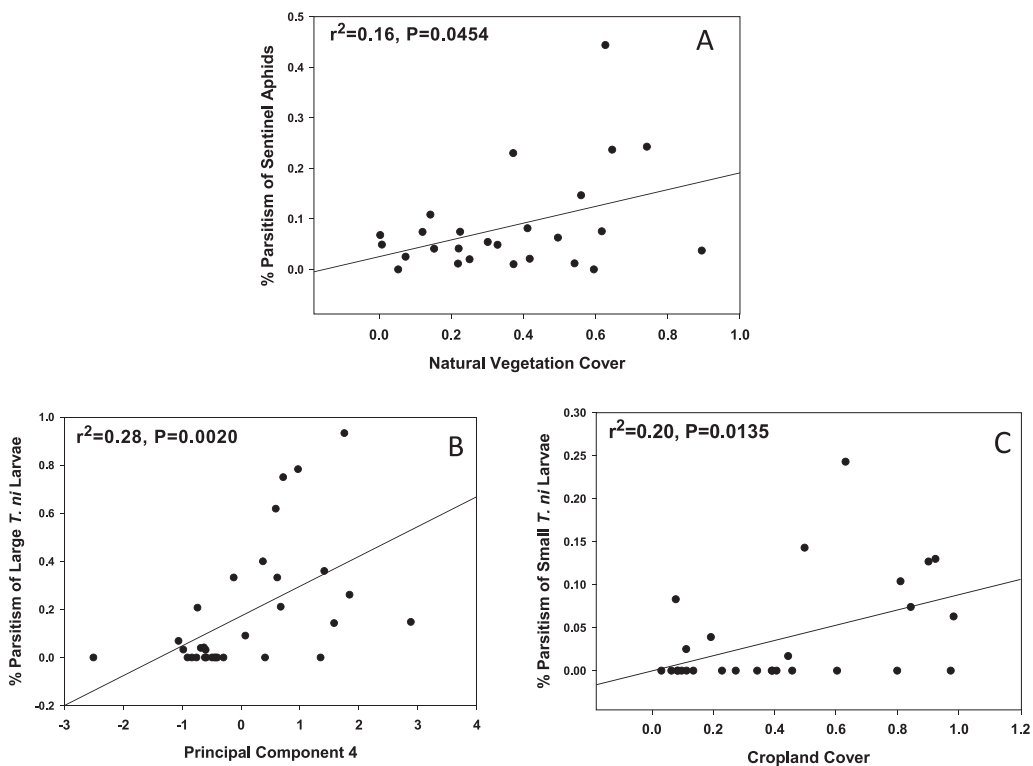


Figure 3 Associations between parasitism of sentinel pests and aggregated vegetation features within 500m of vegetable fields.

Plots showing significant positive correlations between natural vegetation cover in the 500m surrounding the vegetable field and parasitism rates for sentinel *Brassica brevicoryne* (cabbage aphids) in spring 2006 (A), between principal component 4 with high loadings on oak habitats and larger, later instars of *Trichoplusia ni* (cabbage looper) sentinels (B), and for small, early instars of *T. ni* (cabbage looper) sentinels with cropland cover (C), the latter pattern owing to parasitism by the dominant braconid parasitoid *Microplitis alaskensis*.

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Table 4. Associational patterns between the percentage of recovered sentinel pests hosting different taxa of parasitoids and the percent cover of cropland, natural vegetation and riparian vegetation and the first four principal components for plant groups within 500 meters^a

Vegetation variables & stats	Aphids May	Aphids Aug	Large <i>T. ni</i>	Small <i>T. ni</i>	Small <i>T. ni</i>
	braconids	braconids	tachinids	ichs + bracs	<i>M. alaskensis</i>
Cropland					
R	-0.3322	-0.1460	-0.2926	0.4610	0.41213
P-value	0.0973	0.4177	0.1041	0.0135	0.0327
Natural					
R	0.3957	0.1703	0.1681	-0.4838	-0.4252
P-value	0.0454	0.3434	0.3577	0.0091	0.0270
Riparian					
R	0.2117	-0.0370	-0.0848	-0.1428	-0.1533
P-value	0.2991	0.8381	0.6444	0.4685	0.4452
PC 1					
R	0.2088	-0.1969	-0.1251	-0.0122	0.0125
P-value	0.3060	0.2722	0.4953	0.9508	0.9508
PC 2					
R	0.1459	0.0513	-0.0731	-0.1648	-0.1892
P-value	0.4769	0.7766	0.6910	0.4021	0.3446
PC 3					
R	0.1350	0.0168	0.0303	-0.3747	-0.3396
P-value	0.5107	0.9262	0.8693	0.0495	0.0831
PC 4					
R	-0.0970	0.3973	0.5247	-0.1043	-0.1256
P-value	0.6374	0.0221	0.0020	0.5973	0.5325

^a With significantly positive or negative associations indicated in bold font.

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Of 2040 late instar (large) *T. ni* larvae exposed in farm fields, 828 (41%) were not recovered, presumably due to predation (except for a few found in moats) because isolation reduced the chances of larval escape. Parasitism averaged 18.1%, ranged from zero to 93% per field, and was due to six tachinid species (*Madremya saundersii* Williston, *Voria ruralis* (Fallén), *Lespesia archippivora* Riley, *Compsilura concinnata* (Meigen), *Siphona plusiae* (Coquillett), and *Eucelatoria armigera* (Coquillett)). We detected a non-linear, step-wise increase in mean parasitism rates of these larvae (significant threshold effect) as the percent cover of natural vegetation within 500m exceeded 30%. Mean parasitism in fields with less than 30% natural habitat was 4.3% compared to 27.5% parasitism in fields with greater than 30% natural vegetation in the landscape (Kruskall-Wallis, $X=6.77$, $P=0.0093$). Also, the percentage of recovered larval mortality due to tachinid parasitism, for these late instar *T. ni* was positively associated with PC4 (Fig. 3B, Table 4), which has a very high positive loading on oak-dominated woodlands.

In contrast to the dominance of tachinid parasitoids on large larvae, the small *T. ni* larvae exposed in farm fields were primarily parasitized by wasps. Of 3480 first and second instar *T. ni* larvae placed on potted plants in September 2007, 1088 (31%) were not recovered. Parasitism rates on recovered larvae were low, averaging 5.2% of reared larvae per farm, ranging from zero to 24%. Reared parasitoids included two braconids (*Microplitis alaskensis* Ashmead and *Cotesia* sp.) and three ichneumonids (*Hyposoter exiguae* (Viereck), subfamily Campopleginae, *Therion californicum* Cresson in the subfamily Anomaloniinae, and an unidentified species in the subfamily Ichneumoninae). This was the first record of *T. californicum* reared from *T. ni*. In contrast to the positive associations with natural habitat or elements of natural habitat (PC4) shown with *T. ni* parasitism by tachinids, aphid parasitism, and the general diversity of parasitoids collected in these fields, the parasitism rate of early instar *T. ni* showed a *positive* relationship with cropland cover (Fig. 3C) and a strong *negative* association with the cover of natural vegetation (Table 4). These associations were likely driven by a braconid wasp *M. alaskensis*, which was reared from the majority (58%) of parasitized sentinel larvae exposed as 1st or 2nd instars (Table 4).

Discussion

An impressive number of parasitoid species are associated with California organic vegetable fields, with ca. 300 species captured during our study, and we reared 13 species of parasitoids from a single pest species (cabbage looper) exposed to parasitoids in these fields. We call attention to the potential loss of biodiversity in this group of mostly beneficial insects with the removal of non-crop vegetation or with future intensification, based on a robust and repetitive pattern of higher parasitoid richness and diversity in farm fields that had a greater percentage of surrounding landscape in riparian or other natural habitats, and lower parasitoid richness and diversity in farm fields within more intensified farming areas, with higher percentages of cropland cover. This pattern for parasitoids captured in July 2005 held true for all parasitoids together, for different parasitoid families, and for specialists and generalists on different types of host arthropods, some of which include major crop pests. Our results are consistent with abundance and richness patterns for natural enemies in other studies of farmland intensification (Chaplin-Kramer et al., 2011; Inclán et al., 2015). They support our prediction that landscapes with persistent vegetation can augment the biodiversity of beneficial insects and potential for biological control services, and bolstered our concerns about a cost to vegetation eradication and cropland expansion. That is, conservation biological control depends on having enough individuals of enough species of naturally occurring enemies of crop pests to regulate pest populations, yet most species of parasitoids require resources beyond those provided in the crop field or nearby constellation of similar crops.

Less frequently disturbed, non-crop habitat is likely to provide a refuge in terms of alternate hosts, a variety of food resources for adults (e.g. flowers (Tooker et al., 2006), and undisturbed pupation sites (Landis et al., 2000; Olson and Wackers, 2007)). For example, the tachinid *S. plusiae*, which attacks noctuid moth larvae that include crop pests, uses *Phryganidia californica* Packard as an alternate host, a common and occasionally outbreaking lepidopteran that feeds on coastal oak foliage. Indeed, we found a significant positive association between the cover of oak woodlands in the landscape and parasitism rates of sentinel *T. ni* cabbage loopers placed in these fields. The ichneumonid *Diadegma insulare* (Cresson), an important biological control agent of diamondback moth larvae *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) in cole crops, would likely find enough hosts in annual crop fields most of the year, but may also rely on cruciferous weeds in coastal grasslands or nectar sources in semi-natural woody vegetation. Parasitism rates for both of these pests were shown to be positively related to forest cover and forest perimeter in the landscape (Bianchi et al., 2008). The aphidiine *D. rapae*, a prominent parasitoid of *B. brevicoryne* cabbage aphids, commonly attacks aphids associated with cultivated crucifers, and may build up over the winter on wild radish and wild mustards within and along the edges of coastal prairie vegetation. If so, these plants may also be a source pool for pestiferous aphids. However, *D. rapae* attacks aphid hosts not only on non-crop Brassicaceae, but on Chenopodiaceae, Solanaceae, Liliaceae and Asteraceae (Pike et al., 1999). Although the majority of parasitoid species captured in organic crop fields are likely to encounter at least some suitable host taxa in the farm environment, some portion of the increased richness associated with natural habitat was likely due to transient parasitoids passing through crop fields between their nearby non-crop habitats. For example, the tachinid *Protodejeania echinata* Thomson, oviposits in hosts that do not feed on cole crops, like the western tussock moth *Orgyia vetusta* Boisduval (Lymantriidae), which feeds on oaks, lupines and fruit trees in coastal California.

A meta-analysis by Chaplin-Kramer et al. (2011) showed a dearth of studies demonstrating that prominent landscape effects on parasitoid abundance and richness result in enhanced biological pest control. Sentinel pest trials are useful for comparing parasitism frequency in the field under different conditions, but they are laborious and limited in scope. By necessity, these trials are snapshots of parasitoid activity associated with a few hosts deployed at a certain density in crop fields that may differ in their background host densities. Although they provide relative measures of parasitism rates in fields with different levels of resident parasitoid diversity, they can be confounded by the timing of the test, overall host densities, and the composition of the resident parasitoid community. Wholesale collection and rearing of naturally occurring pests is a better measure of absolute levels of biological control, but comparisons among farms are not possible when pest densities vary widely. We recognize that while percent parasitism is a reasonable measure of ecosystem services, determining the impact of increased parasitism on maintaining pests below an economic threshold was beyond the scope of this study.

The frequency of parasitism on our sentinel pests was relatively low on average, but over 90% of sentinels were parasitized in some fields, despite short exposure times of two (aphids) or five (loopers) days. Significant relationships among sentinel parasitism rates and landscape vegetation were present in all cases, but they were not necessarily consistent with summer parasitoid richness patterns. Aphidiine parasitism of aphids in spring was positively correlated with natural habitat, as was species richness and diversity of that parasitoid group. Parasitism of late instar *T. ni* also showed a positive relationship with natural vegetation, but it was non-linear, such that tachinid parasitism rates were high, on average, when natural vegetation cover exceeded 30% (also see Letourneau et al., 2012). Aphidiine parasitism of sentinel aphids in August did not match richness or landscape - diversity patterns for those taxa as measured earlier that season, and the opposite trend occurred for mortality of early *T. ni* sentinels caused by parasitoids. Both the ichneumonid *H. exiguae* and the braconid *M. alaskensis* tended to be more active in landscapes with annual crops (Bothwell, 2012),

possibly because crop fields offered a higher concentration of preferred hosts. A range of outcomes is not surprising if parasitism of each host or host stage is largely due to one or a few species that may have specific habitat and/or resource requirements (e.g., for alternative hosts).

We might expect parasitism to parallel the relationships between landscape factors and parasitoid richness if the frequency of parasitism were integrated across all potential hosts in the organic field. Incidentally, the prevailing trends of higher parasitoid richness with more non-crop habitat in our study were likely to hold for hyperparasitoids that attack parasitoids of crop pests and parasitoids of important predatory insects, such as syrphid flies that feed on aphids. Any intraguild predation would have been integrated into the relative parasitism rates we found in different fields. Overall, a higher percentage of natural or riparian habitat nearby may provide better “insurance” for the delivery of ecosystem services under environmental variability (Hooper et al. 2005, Letourneau et al., 2009). That is, when some level of functional redundancy is retained among the natural enemy community, conditions adverse to a dominant parasitoid species may be less detrimental to other species that can suppress crop pests in their absence (Menalled et al., 2003). For example, the maintenance of natural and riparian vegetation with its associated diversity of aphidiines, could increase the chance of other parasitoids contributing to aphid parasitism should the common *D. rapae* undergo interannual variations in density, changing climatic effects (Gillespie et al., 2012; Klaiber et al., 2013), unusual pressure from hyperparasitoids or disruption from insecticides or other materials applied to vegetable fields (Prado and Frank, 2013).

Whereas the central coast of California provides a model of agricultural production within a diverse landscape mosaic, the 2006 discovery of a deadly strain of *E. coli* in spinach caused a shock to farm conservation practices. Pressure was brought by processors and retailers to keep wildlife out of production fields by removing non-crop vegetation around farm fields. Between 2005 and 2012, the amount of natural vegetation within 50m of the edge of crop fields had decreased by up to 30%, riparian vegetation coverage had fallen by up to 6% and cropland had increased in the 50m surrounding fields by up to 30% in the Salinas valley region (Karp, 2015). Despite these measures carried out by growers in hopes of reducing microbial food contamination events, Karp et al. (2015) found an increase in the incidence of enterohemorrhagic *E. coli* on leafy greens with the removal of natural vegetation. Furthermore, enterohemorrhagic *E. coli* was not influenced by the removal of riparian vegetation, and increased with an increase in cropland around the farm field compared with the levels in 2005. We used the same habitat categories in our study to provide parallel information on the losses to biodiversity conservation predicted by Sutherland et al. (2012) from ‘sterile farming’ policies, specifically parasitoids, that deliver ecosystem services. Our demonstration of positive relationships between parasitoid diversity and natural or riparian vegetation around farms and a negative relationship with increased cropland suggest that vegetation removal and cropland intensification had additional costs to farmers, and support the conclusions of Marino et al. (2006) about the key role of the maintenance or restoration of late successional habitats for the conservation of native parasitoids. Ecological research in agriculture is foundational for the integrated science and policy needed to transform food production systems for improved food security, public and environmental health.

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Contributions

- Contributed to conception and design: DKL, SGBA
- Contributed to acquisition of data: SGBA, DKL, RRR, MJS, JOS
- Contributed to analysis and interpretation of data: DKL, JOS
- Drafted and/or revised the article for intellectual content: DKL
- Approved the submitted version for publication: DKL, SGBA, RRR, MJS, JOS

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Competing interests

The primary author was invited to submit original research for a forum on agroecology solutions; none of the authors have professional, financial, personal or other conflicts of interest that would bias the collection or interpretation of data for this publication.

Data accessibility statement

A reference collection of ichneumonid wasps is curated by the University of California, Santa Cruz Natural History Museum, and data on parasitoid richness and abundances used in this publication are part of a larger database housed at the Environmental Interactions Lab at UCSC. Contact D.K. Letourneau to discuss and/or arrange to access these resources.

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