Journal of Applied Ecology

Journal of Applied Ecology 2012, **49**, 1405–1416 doi: 10.1111/jpe.12001

Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops

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Summary

1. Agricultural intensification has led to the removal of semi-wild, perennial vegetation in agricultural landscapes. However, in short-cycle crops, frequent disturbance from insecticides, harvesting and tillage disrupts the establishment of resident communities of natural enemies of pests. Semi-wild perennial vegetation may provide critical habitat for mobile arthropods supporting ecosystem services and sustainable agriculture.

2. We sampled tachinid parasitoids, an important taxon for biological control of vegetable pests, in 35 organic farm fields situated within a mosaic of agricultural, residential and preserved lands in coastal California. Using a GIS, we characterized land-use and vegetative cover within 500 and 1500 m, including grasslands, chaparral, oak woodlands and coniferous forests.

3. The abundance and species richness of tachinid flies captured in Malaise traps in spring and summer were positively associated with the cover of semi-wild perennial vegetation, especially in mesic habitats. The effective number of tachinid species (e^H) was correlated positively with semi-wild perennial vegetation cover and negatively with annual crop cover in the landscape in September and May.

4. The richness of parasitoids emerging from sentinel lepidopteran pests exposed on potted plants within farm fields was negatively associated with annual cropland cover. Parasitism rates dropped precipitously as percentage annual crop cover exceeded species-specific thresholds.

5. *Synthesis and applications*. Maintaining semi-wild, perennial habitat fragments as refugia to support parasitoids can increase biodiversity and provide ecosystem services in annual and short-cycle crop fields. Our results indicated that crop pests escaped parasitism by two important tachinid species in landscapes with greater than 38% and 51% cover of annual cropland, respectively. Landscape-level research is critical for integrating science and policy to conserve biodiversity, promote sustainable agroecosystems and evaluate new anti-wildlife vegetation removal campaigns that may harm biological control agents while targeting microbial food contamination.

Key-words: annual crops, biodiversity, biological pest control, Diptera: Tachinidae, ecosystem services, GIS, landscape complexity, organic farming, sentinel pests

Introduction

The capacity for ecosystem services to improve U.S. agriculture production and profitability is well-established (Daily *et al*. 1997; Losey & Vaughan 2006), leading to serious concerns about the negative consequences of agricultural intensification (Butler, Vickery & Norris 2007; Power 2010). For over a decade, major research and policy initiatives in the United States and Europe have targeted sustainable crop production and biodiversity conservation (Balvanera *et al*. 2001; Bianchi, Booij & Tscharntke 2006). Traditionally, pest management has focused on field level interactions among particular crops, pests and their natural enemies, yet dispersal, colonization and foraging patterns of insects occur across a range of scales. Ecologically based strategies for pest control that optimize ecosystem services expand the scope of insect pest regulation from the curative control of single pest populations to management of multi-trophic food webs (NRC 1996) and the scale of biodiversity conservation to working landscapes (Thies, Steffan-Dewenter & Tscharntke 2003; Tscharntke *et al*. 2008). Innovative vegetation management on farms and

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their surroundings are necessary for improving biological control of crop pests, thus reducing grower dependence on pesticides, and benefitting both agriculture and the environment (Nicholls & Altieri 2007; Landis *et al.* 2008; Zhang, Werf & Swinton 2010; Meehan *et al.* 2011).

Theoretically, landscape heterogeneity helps maintain long-term ecological function in highly disturbed agroecosystems (Tscharntke *et al.* 2008). The role of habitat stability for natural enemy efficacy in biological control is well-recognized (Southwood 1977; Geiger, Wackers & Bianchi 2009), making annual and semi-annual cropping systems particularly vulnerable to insect pest outbreaks (Wiedenmann & Smith 1997; Letourneau & Altieri 1999). The high frequency and intensity of disturbance (tillage, bare fallow, short cycle harvests) disrupts community development and suppresses local source pools of natural enemies. Natural enemy habitat is degraded through removal of their food and shelter resources (Landis & Menalled 1998; Letourneau 1998) forcing beneficial insects into patterns of 'cyclic colonization' from refuge habitats (Wissinger 1997). Ultimately, the degree to which the habitats within the mosaic are favourable to herbivores and their natural enemies, coupled with enemy propensities for movement, largely determines the abundance and diversity of beneficial insects and the potential for natural enemies to control herbivore populations in crop fields (Barbosa & Benrey 1998). Thus, conservation biological control through the conservation, restoration or establishment of on-farm or surrounding vegetation is a promising strategy (Ehler 1998; Thies, Steffan-Dewenter & Tscharntke 2003; Landis *et al.* 2005) that requires investigation (Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011). However, new procedures to reduce the probability of pre-harvest microbial contamination in freshwater produce after a 2006 disease outbreak caused by *Escherichia coli* (Migula) Castellani and Chalmers O157-H7 in California spinach include non-crop vegetation removal to reduce wildlife movement into agricultural fields. Despite little consensus on the roles of birds, bats, deer or rodents as potential vectors of crop-borne *E. coli*, and the potential for non-crop vegetation to act as refugia for biological control agents in ephemeral crops, sterile farming standards for food safety are under consideration in the USA and other countries (Sutherland *et al.* 2012). Evaluating potential biological control losses of these sterile farming standards is critical to determining whether and how they should be implemented.

To examine associations among semi-wild vegetation in agricultural landscapes, on-farm insect biodiversity, and biological control, we measured the species richness and abundance of parasitoid flies in the family Tachinidae in annual vegetable fields, with surrounding landscapes ranging from complex vegetation mosaics to homogeneous areas of agricultural production in the central coast region of California. Annual vegetables are among the most highly disturbed (frequent tillage) and pesticide-intensive production systems; thus, the potential benefits of reduced pesticide dependence are considerable. Tachinids are a ubiquitous, diverse (*c.* 10 000 described species) and ecologically important group of parasitoids, yet relatively little is known about how tachinid diversity varies among habitats (Stireman 2008), their effectiveness as natural enemies in natural and managed habitats (Weseloh 1982; Felland 1990), their importance as pollinators (Rader *et al.* 2011), or what factors may enhance the services they provide in agroecosystems.

Complexity of agricultural landscapes should theoretically be associated with an increased diversity of beneficial insects including parasitoids (Marino, Landis & Hawkins 2006; Tscharntke *et al.* 2008; Chaplin-Kramer *et al.* 2011); therefore, we hypothesized that tachinid fly diversity would increase with landscape complexity. Specifically, we addressed the following three questions: (i) is the abundance and species richness of Tachinidae visiting annual vegetable crops associated with the cover of perennial vegetation or richness of semi-wild vegetation in the surrounding landscape? (ii) Which specific vegetation types are associated with the abundance of tachinid parasitoids in crop fields, especially those species known to use pest insects as hosts? and (iii) Does tachinid fly parasitism on a sentinel pest reflect fly abundance and species richness patterns or landscape vegetation characteristics?

Materials and methods

STUDY SITES

Tachinid fly richness and parasitism levels were measured in certified organic crop fields located on coastal terraces and valleys within approximately a 50 km (north–south) by 30 km (coast–inland) area representing central coast farming in California (Fig. 1a). Monterey, Santa Cruz and San Benito counties support a high diversity of native plant species in a mosaic of wetlands, chaparral, oak woodlands, coastal prairies (Press, Doak & Steinberg 1996) in landscapes also featuring agricultural operations. Monterey County alone accounts for *c.* 10% of the nation's market value for vegetable production (USDA 1997). Our sample fields represented land under production by 25 of *c.* 50 vegetable growers listed in the California Certified Organic Farming membership directory for the Monterey Bay region, and met the following criteria: willingness of growers to participate, fields included cole crops or lettuce, and sites were separated by at least 1 km. Crop fields had vegetable rotations (including up to 10 varieties of broccoli, cabbage, kale or other cole crops, lettuces, mixed cropping of melon, squash, cucumbers, carrots and tomato), horticultural crops and occasionally a strawberry rotation; we used an index of 1–4 to rate in-field crop diversity in ascending order for monoculture, *Brassica* and *Lactuca* crops, three to four plant families, and more than four plant families.

Fields were embedded in landscapes ranging from primarily homogenous cover of annual crops (Fig. 1b) to a more diverse array of vegetation types and other land uses (Fig. 1c).

Using colour-infrared and black-and-white orthophotos in a GIS, we characterized, manually digitized, and measured vegetation cover within a 1·5-km radius circle (*c.* 7 km^2) from the centre of each of 35 fields; this area around the field centre and a

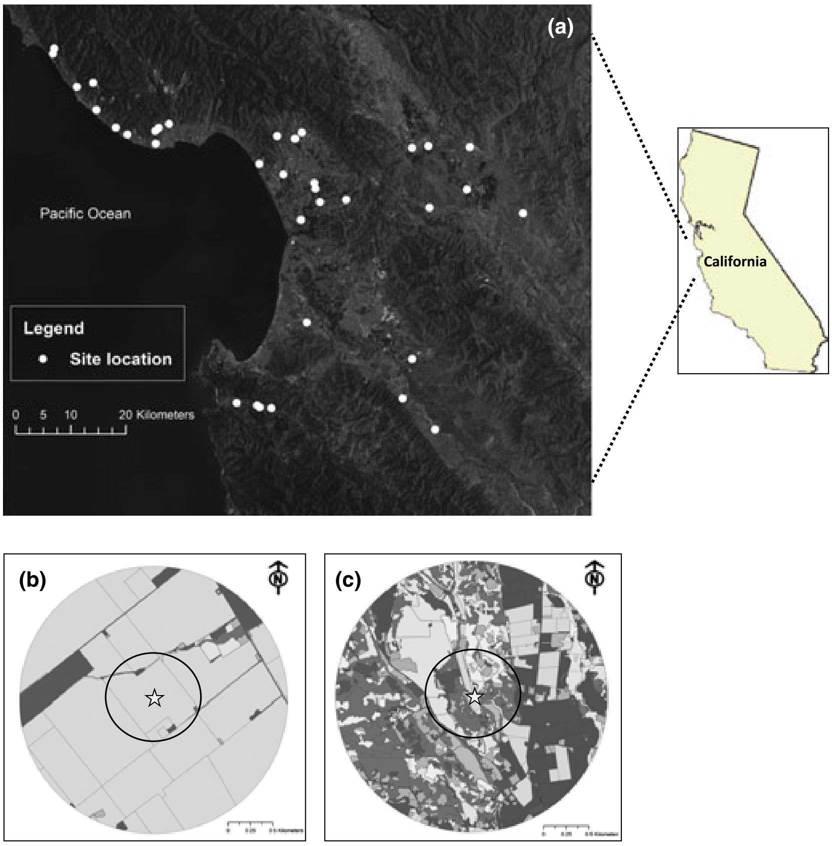

Fig. 1. (a) Map of California with location of 35 certified organic vegetable production fields in Santa Cruz, Monterey and San Benito Counties on the Central Coast and GIS vegetation and land-use maps for annual crop fields with comparatively low (b) and high (c) landscape complexity within 0.5 km (black circle) and 1.5 km (outer margin) of the field centre (star).

smaller landscape scale (0·5-km radius) were based on estimates of scales relevant to the movement of many beneficial insects from source pools by Letourneau & Goldstein (2001) for herbivores, predators and parasitoids, Thies, Steffan-Dewenter & Tscharntke (2003) for herbivores and parasitoids, and Kremen *et al.* (2004) for native bees. It is clear that tachinids possess relatively strong dispersal potential, over several kilometres (e.g. Munro 1998). However, typical trivial movement distances are unknown and are likely to be variable among species in such a large and diverse group. The few studies from which such inferences can be extracted suggest that 'typical' movement of individuals might be on the scale of hundreds of meters (Brodmann, Wilcox & Harrison 1997; Roth, Roland & Roslin 2006; Rader *et al.* 2011). Thus, landscape characteristics within 0·5 km may be the most relevant scale, but both scales are likely within the potential dispersal range of many tachinids.

We evaluated over 30 landscape categories, including types of woody vegetation (trees in the genera *Acacia*, *Alnus*, *Laurus*, *Eucalyptus*, *Quercus*, *Salix,* conifers, *Baccharis, Toyon, Salvia Artemisia* and other chaparral genera, *Manzanita*, *Rubus* and hedgerows), annual forbs and grasses, mixed land uses (residential, rural, parkland), agricultural fields (annual crops, perennial crops) and non-vegetated cover (gravel, paved road, industrial, ocean, freshwater). For this analysis, we grouped finer categories into larger categories such as semi-wild perennial and annual vegetation, and non-vegetated cover, and enumerated semi-wild vegetation richness, for a total of fourteen vegetation and land-use variables listed in the caption in Table 1.

INSECT SAMPLING

Tachinid flies were collected in July and September 2005 and May 2006 using a Malaise trap (BioQuip model 2875AG; 1·2 m wide × 2·13 m tall, with forest green netting) placed for 48 hours in the centre of each of the 35 crop fields. 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 (Ottawa, Canada), or if unidentifiable, designated with a code (e.g. females of some species, damaged). We also categorized tachinid species by host taxa, host range (i.e. specialists whose hosts are within one family or generalists with hosts in > 1 family) and whether they are likely to attack local crop pests or non-pests based on host records in Arnaud (1978) and more recent taxonomic literature (e.g. O'Hara 1992, 1996, 2002). In cases where hosts were unknown, we assumed that the species was relatively specialized. When the species was uncertain or records did not exist, designations were inferred from the genus to which the species belonged.

SENTINEL EXPERIMENT

To determine whether trends in tachinid fly abundance and diversity were indicators of pest parasitism and the richness of parasitoids causing this mortality, we used *Trichoplusia ni* (Hübner) larvae (Lepidoptera: Noctuidae) as sentinel pests in summer (July, $n = 19$ farm fields in Santa Cruz county only, due to limited number of sentinel larvae) and autumn (September, $n = 35$)

Table 1. The 0.5-km radius landscape variable loadings on PCA axes 1–7 and the percentage variance explained by each principal component, by the percentage cover of semi-wild annual and perennial vegetation, annual crops, conifers, coyote brush, *Eucalyptus*, suburban residential buildings and yards, isolated rural buildings and yards, oak woodlands, perennial crops, riparian and marsh, sage brush and wild vegetation richness*

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% variation	26·6	15·9	11·6	9·2	7·3	6·8	5·7
wannveg	0·1937	−0·2682	**0·4678**	0·1753	0·0297	0·2448	−0·3892
wprnveg	**0·4133**	**0·3720**	0·0166	−0·1353	0·0358	0·0420	−0·0179
Anncrp	−**0·4711**	0·0579	−0·0901	−0·0172	−0·3131	−0·1526	−0·0544
Conifer	0·2519	**0·4677**	−0·1256	−0·2069	0·1987	−0·0310	0·0121
coycomp	0·2397	**0·3768**	0·2432	−0·0034	0·0065	0·0442	−0·1557
Euc	0·2235	−**0·3612**	−0·2250	−0·0993	−0·1572	0·2173	−**0·4740**
Resid	0·2479	−0·3252	−0·2149	−0·1468	−0·1182	−0·0321	**0·4994**
Rural	0·2457	0·0894	−0·3248	**0·4110**	−0·1411	−0·0633	0·1694
oakcomp	**0·3503**	−0·1936	**-0·3167**	−0·1126	−0·2249	0·1115	−0·0189
Prncrp	−0·1367	0·0542	−0·1446	0·2789	0·3098	**0·7976**	0·2559
Nonveg	−0·0602	−0·2863	0·1200	−0·4102	**0·5926**	−0·0785	0·1705
Wetrip	0·0566	−0·0929	−0·1834	**0·6213**	**0·4261**	−**0·3873**	−0·1475
sagcomp	0·1028	−0·0397	**0·5329**	0·2455	−0·3238	0·0277	**0·4262**
Numveg	**0·3439**	−0·2209	0·2058	0·0492	0·1323	−0·2329	0·1405

Strong variable loadings are highlighted in bold.

*Cover categories are: wprnveg = non-crop/semi-natural perennial vegetation including chaparral, coastal scrub, willow, *Eucalyptus*, conifer, blackberry, poison oak, ice plant and coffee berry; wannveg = coastal meadows dominated by grasses that dry out in late spring and forbs such as spring–summer flowering wild radish, hemlock and native soap plant; anncrp = annual crop (lettuce, broccoli, strawberry, corn, etc.); coycomp = chaparral and seasonally dry (summer, autumn) grasslands dominated by native, evergreen coyote brush which blooms in October–December; euc = winter blooming *Eucalyptus* trees; resid = residential areas often with watered, flowering forbs, bushes and trees; nonveg = unvegetated industrial areas or roadways, oakcomp = oak woodlands, prncrp = perennial crops (orchards, vineyards), wetrip = open water, marshland and riparian vegetation (such as willows); sagcomp = sage brush dominated chaparral or grassland, numveg = number of vegetation types represented.

2005. This ubiquitous pest of cole crops and lettuce frequently hosts specialist and generalist tachinid parasitoids, including *Voria ruralis* (Fallén)*, Siphona plusiae* (Coquillett)*, Madremyia saundersii* (Williston) and *Eucelatoria armigera* (Coquillett), which have been reared from *T. ni* collected as 3rd to 5th instars (Oatman 1966; Clancy 1969). Tachinid oviposition on *T. ni* has been studied on *V. ruralis,* which parasitizes second to fifth instar larvae, but survives best on 2nd to 4th instars (Elsey & Rabb 1970) and the introduced species *Compsilura concinnata* (Meigen), which parasitized 2nd to 4th instars, preferring older larvae (Caron, Myers & Gillespie 2010).

In summer, sentinel *T. ni* were reared from field collected adults and protected from parasitism in rearing cages until field exposure, with three 2nd to early 4th instar larvae distributed among each of eight potted collards, which were placed regularly among the centre rows of cole, lettuce and mixed vegetable crops. In autumn, six unparasitized, 3rd instar larvae purchased from Bio-Serv^{TM} (Frenchtown, New Jersey, USA) were placed on each of 10 plants. Each plant was placed into a large, water-filled tray to supply water and prevent larval escape, covered with 1 cm^2 bird-netting to deter insectivorous birds, and placed out of contact with crop foliage. After seven days of field exposure, collard plants were collected and all recovered larvae, usually 5th instars, were reared individually in Bio-Serv^{TM} trays on generalized lepidopteran diet and a 16:8 h light/dark cycle. We recorded the fate of each of the 24 (summer) or 60 (autumn) larvae per farm field as: *T. ni* adult, Tachinidae (number and species emerged), death by virus (field infection), unrecovered (due to field predation or escape), non-emergence from pupa, or, rarely, dead from an unknown, non-viral cause, lost in the laboratory, or the single emergence of a hymenopteran parasitoid. We estimated mortality of *T. ni* due to parasitism by Tachinidae as the proportion of live pupae producing flies and identified emergent flies as described for Malaise trap samples.

DATA ANALYSIS

To determine whether the abundance or richness of tachinid parasitoids was associated with the 14 landscape variables (described earlier) within a 0·5-km and/or 1·5-km area, Pearson's correlation coefficients were calculated on means per farm field with PC-SAS version 9.2 (SAS Institute, Inc., Cary, North Carolina, USA). We also used the effective number of species (e^H) (MacArthur 1965; Jost 2006) to clarify the effects of landscape variables on tachinid species diversity because richness was unlikely to be independent of abundance (or trap sample size) despite our equal sampling effort. Because many of the landscape variables were positively or negatively correlated with one another, we examined their combined influence on tachinid communities as principal component axes using R 2.10 (R-Development-Core-Team 2009). All principle components that explained at least 5% of the variance in land-cover categories among farms (PC1–PC7) were used for summer, autumn and spring as predictors of abundance, species richness and diversity of Tachinidae for each field using Generalized Linear Models (GLMs). For richness and abundance measures, negative binomial GLMs were employed due to overdispersion using the R package *MASS* (Venables & Ripley 2002) and stepwise model selection (forward and backward) was performed in all analyses based on AIC scores using the *step AIC* function in *MASS*. We constructed parallel GLMs with stepwise

AIC model selection for the habitat variables used in PCA analyses. Additional analyses were conducted to examine how PCA and habitat variables might differentially affect the abundance of only generalist tachinids, only specialists and only tachinids known to or likely to attack pest species. Due to the large number of comparisons, and the dependencies of some tests, we employed Holm's method of sequential Bonferroni corrections (Holm 1979) to assess statistical significance of variables for each data set. This correction is highly conservative in guarding against type I error.

We tested whether greater tachinid abundance or richness in fields (all species and the six most common species individually) resulted in higher sentinel caterpillar parasitism in the summer and fall experiments with simple regression models. Effects of landscape variables on sentinel parasitism were also examined with general linear models (as earlier). Plots of parasitism levels of sentinel caterpillars against annual crop coverage indicated a threshold pattern such that tachinids never achieve high parasitism when annual crop cover is extensive. To visualize this pattern, we fitted local second-order polynomial regression lines (loess in R) to total parasitism and for parasitism by the two most important parasitoids, *Voria ruralis* and *Madremyia saundersii.* Given the apparent step-like nature of the relationship, we used regression tree models (R package *tree*) to estimate the threshold in annual crop coverage that explains the maximal variance in parasitism. We used these estimated thresholds to compare parasitism in fields with low vs. high crop coverage with nonparametric Kruskal–Wallis tests due to violations of normality. We focused our analyses on the autumn data set because none of the experimental sites tested in summer had a high degree of annual crop cover.

Results

LANDSCAPE COMPLEXITY

The cover of annual cropland within 0·5 km of the field centre ($n = 35$) varied from 3% to 97% (1–90% for 1·5-km radius landscape); semi-wild (non-crop) perennial vegetation cover ranged from 0% to 82% (1–90% for 1·5-km scale). The number of semi-wild vegetation types present (vegetation richness) varied from 0 to 13 (1–14 for 1·5-km scale) (Fig. 1b&c). We report the 0·5-km results unless associational patterns were substantially different for 1·5 km. The first seven principal components explained approximately 83% of the variation in landscape cover surrounding the sampled fields (0·5 km radius, Table 1; and 91% for 1·5 km radius, with similar loadings, see Appendix S1 in Supporting Information). The first axis (PC1) has large positive eigenvalues for the cover of semi-natural perennial vegetation, oak woodland and vegetation richness, and negative eigenvalues associated with annual crop cover, suggesting that it reflects the degree of disturbance, at least in part (Table 1). PC2 similarly has large positive loadings for semi-natural vegetation, this time coupled with conifer and coyote brush *Baccharis pilularis* DC. and with large negative values for *Eucalyptus* and residential lands. Subsequent PCA axes are less easily interpreted, although PC3 is associated with large positive eigenvalues of more xeric vegetation (seasonally dry grasses and sagebrush *Artemisia* spp.).

TACHINID RICHNESS AND ABUNDANCE

Malaise trap captures in 35 organic farm fields averaged 22·6 tachinid flies per 48-hr sample per field, yielding 2078 tachinid flies belonging to at least 29 species in July 2005, 187 tachinids representing 22 species in September 2005, and 90 tachinids in 18 species in May 2006 (Appendix S2). Five unidentifiable specimens were excluded from the analyses. At least 39 species were captured over all samples, with a grand mean richness of four species per 48-hour sample. Of the ten most common species, at least seven use agricultural pests as hosts (Appendix S2, asterisks). The samples were dominated, however, by a small number of common species (*Siphona plusiae*: 69% of total captures, *Eucelatoria armigera*: 11%*, Periscepsia helymus* (Walker): 5%, and *Triarthria setipennis* Fallén: 4%). Except for *T. setipennis*, these common species deposit incubated, macro-eggs on lepidopteran larvae, including noctuid moth species that feed on vegetables. The remaining 35 species were each represented by fewer than 10 individuals.

ASSOCIATIONS BETWEEN TACHINIDAE AND LANDSCAPE VARIABLES

The hypothesized negative impact of disturbance upon natural enemy communities was supported by significant negative associations between annual crop cover and mean tachinid richness ($R^2 = 0{\cdot}28$, $P < 0{\cdot}0012$) and abundance ($R^2 = 0{\cdot}20$, $P < 0{\cdot}0067$). Those associations were community phenomena, holding when the dominant species, *S. plusiae,* was excluded from the analyses of individual cover variables (mean tachinid abundance positively associated with wild perennial cover, $R^2 = 0{\cdot}44$, $P = 0{\cdot}0004$ and mean tachinid abundance negatively associated with annual crop cover, $R^2 = 0{\cdot}15$, $P = 0{\cdot}0230$). The strongest pattern emerging across the three sampling seasons was the robust positive association of tachinid richness and the abundance of tachinids, whether specialists or generalists, with the first principle component (PC1) for both small- (Tables 1 and 2) and large-scale landscapes (Appendix S3). This component, with high positive loadings for semi-wild perennial vegetation and negative loadings for annual crop cover, explained significant variation in richness and abundance in summer and spring; however, in autumn, only the abundance of specialist tachinids was positively associated with PC1, and the positive trend between PC1 and tachinid richness was not significant (Fig. 2, Table 2). In the summer samples, when tachinid richness was greatest, richness was also significantly positively associated with PC2 (Table 2), consistent with a positive influence of conifer cover, again suggesting the importance of stable, perennial vegetation. Analyses of individual variables consistently supported the positive association of tachinid richness and abundance with perennial and sometimes also with non-crop annuals (except for abundance in autumn). Total cover of semi-natural perennial vegetation was the best single predictor of both mean richness ($R^2_{(0\cdot5\mathrm{Km})} = 0{\cdot}45$, $P < 0{\cdot}0001$; $R^2_{(1\cdot5\mathrm{Km})} = 0{\cdot}40$, $P < 0{\cdot}0001$) and abundance ($R^2_{(0\cdot5\mathrm{Km})} = 0{\cdot}41$, $P < 0{\cdot}0001$; $R^2_{(1\cdot5\mathrm{Km})} = 0{\cdot}42$, $P < 0{\cdot}0001$) of tachinids captured in farm fields (Fig. 3), as well as for mean tachinid species diversity (e^H; $R^2_{(0\cdot5\mathrm{km})} = 0{\cdot}32$, $P < 0{\cdot}0005$; $R^2_{(1\cdot5\mathrm{km})} = 0{\cdot}34$, $P < 0{\cdot}0001$). Effects of landscape PCA axes on diversity (e^H) were qualitatively similar to results for richness (e.g. PC1 was retained in all models; Table 2; Appendix S2), but generally weaker. Positive effects of cover of semi-natural perennial vegetation on tachinid diversity were present ($R^2_{(\mathrm{autumn})} = 0{\cdot}16$, $P < 0.\ 0192$; $R^2_{(\mathrm{spring})} = 0{\cdot}36$, $P < 0{\cdot}0002$) except for in summer ($R^2_{\ (\mathrm{summer})} = 0{\cdot}04$, $P < 0{\cdot}2504$) when a few very abundant and many rare species were captured. Positive effects of non-crop perennials do not extend to perennial crop coverage; in summer, tachinid abundance was negatively associated with this variable.

PCA axes 3–7 explain relatively little variance in tachinid richness or abundance. However, PC3 and PC7, axes for which xeric vegetation has high loadings, appear in several AIC selected models of abundance, in autumn and summer, respectively, suggesting a broad but weak negative association of chaparral vegetation on tachinid communities. This conclusion is supported by negative associations between tachinid abundance and sagebrush communities, with some compensation for PC7, in which residential area also has relatively high loading. However, the abundance of specialists, which otherwise followed the trends of generalists and pest-attacking tachinids, was positively associated with habitats that become xeric (PC3) in summer.

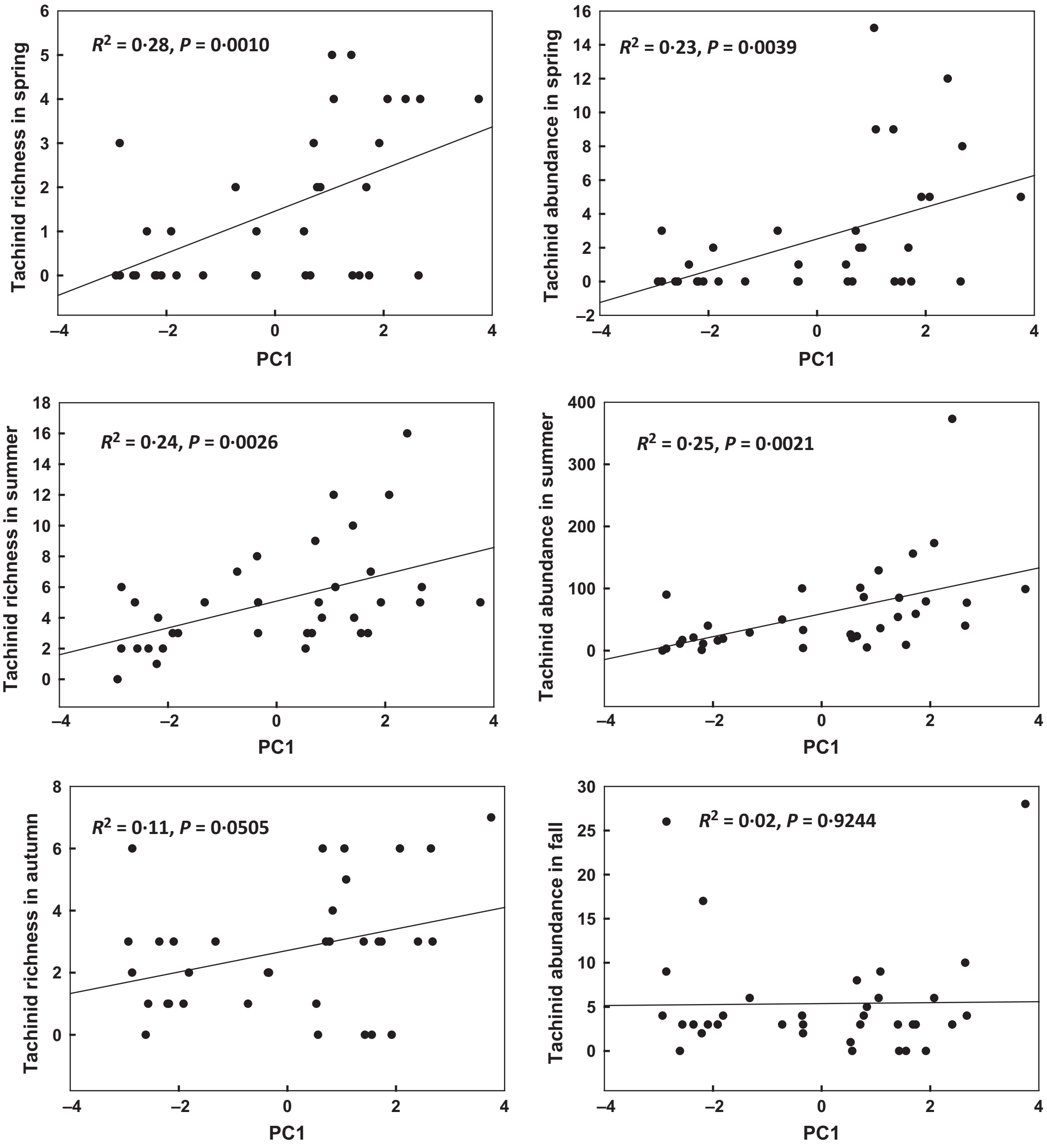

Fig. 2. Relationship between the first principle component (PC1) for landscape (0·5 km) cover variables and the abundance and richness of tachinid parasitoids captured in Malaise traps in summer, autumn and spring samples.

Table 2. Summary of Generalized Linear Models selected by AIC for the analyses employing principal components (left) and specific landscape variables (right) at the 0·5 km scale

Response	PC	Estimate	*P* ≤	Variable	Estimate	*P* ≤
Summer – July 2005						
Richness	1	0·163	**0·0002**	wannveg	1·786	**0·0001**
	2	0·115	**0·0039**	wprnveg	1·843	**0·0007**
	5	0·192	**0·0151**	oakcomp	−2·635	0·0192
	7	−0·214	**0·0128**	prncrp	−3·212	0·1510
				sagcomp	−7·153	0·0090
Diversity	1	0·118	0·1653	numveg	0·104	0·0529
	6	−0·325	0·0573			
Abundance	1	0·380	**0·0001**	wannveg	2·243	0·0198
	6	−0·418	0·0153	conifer	2·256	0·0320
	7	−0·474	**0·0044**	coycomp	5·665	**0·0010**
				prncrp	−9·017	**0·0016**
				wetrip	3·802	0·0435
				sagcomp	−11·157	0·0038
Generalists	1	0·383	**0·0001**	conifer	2·285	0·0328
	6	−0·433	0·0188	coycomp	7·480	**0·0003**
	7	−0·450	0·0110	euc	13·425	0·0649
				resid	1·868	0·1402
				rural	−14·190	0·0919
				prncrp	−7·295	0·0078
				wetrip	4·924	0·0168
				sagcomp	−8·066	0·0395
Specialists	1	0·244	**0·0054**	wannveg	2·534	0·0140
	2	0·174	0·0835	wprnveg	−3·961	0·0500
	3	0·397	**0·0009**	conifer	6·025	0·0166
	7	−0·341	0·0655	coycomp	9·189	**0·0002**
				numveg	0·117	0·0352
Pest enemy	1	0·367	**0·0001**	wannveg	2·111	0·0283
	6	−0·412	0·0159	conifer	2·122	0·0437
				coycomp	5·611	0·0011
				prncrp	−8·932	**0·0018**
				wetrip	3·810	0·0430
				sagcomp	−10·905	0·0047
Autumn–September 2005						
Richness	1	0·106	0·0684	wprnveg	1·614	**0·0018**
	3	−0·195	0·0405	coycomp	−2·877	0·1003
				sagcomp	−6·750	0·1562
Diversity	1	0·354	0·0331	wprnveg	3·445	**0·0177**
	3	−0·369	0·1361	resid	4·523	0·0914
				sagcomp	−11·123	0·1712
Abundance	3	−0·431	**0·0034**	anncrp	1·167	0·0505
	4	−0·246	0·0795	oakcomp	6·132	0·0220
				sagcomp	−10·070	0·1546
Generalists	1	0·106	0·0684	anncrp	0·682	**0·0002**
	3	−0·195	0·0405	sagcomp	2·342	0·1129
				euc	26·810	**0·0033**
Specialists	1	0·294	**0·0018**	wannveg	2·428	0·0553
				conifer	3·034	**0·0055**
				oakcomp	5·871	**0·0011**
				wetrip	3·558	0·1175
Pest enemy	3	−0·366	0·0266	anncrp	1·411	0·0115
	4	−0·370	0·0206	euc	21·025	0·0122
	7	−0·269	0·1614			
Spring–May 2006						
Richness	1	2·770	**0·0008**	wprnveg	2·937	**0·0004**
Diversity	1	0·443	**0·0007**	wprnveg	4·469	**0·0001**
	2	0·292	0·0647			
Abundance	1	0·454	**0·0007**	wprnveg	3·551	**0·0006**
	2	0·216	0·1430	sagcomp	−16·794	0·1529

Table 2. (continued)

Response	PC	Estimate	$P \leq$	Variable	Estimate	$P \leq$
				numveg	0·137	0·0983
Generalists	1	0·415	**0·0122**	wprnveg	3·938	**0·0007**
	2	0·259	0·0998			
Specialists	1	0·405	**0·0042**	wannveg	2·723	0·1323
	2	0·231	0·1160	wprnveg	3·217	**0·0009**
				euc	−19·822	0·1230
				sagcomp	−54·990	0·0820
				numveg	0·1862	0·0543
Pest enemy	1	0·477	**0·0026**	wprnveg	3·482	**0·0024**
				sagcomp	−23·421	0·2105
				numveg	0·146	0·1254

Significant *P*-values after Holm's sequential Bonferroni correction for each data set are indicated in bold. See Table 1 for explanations of variable abbreviations.

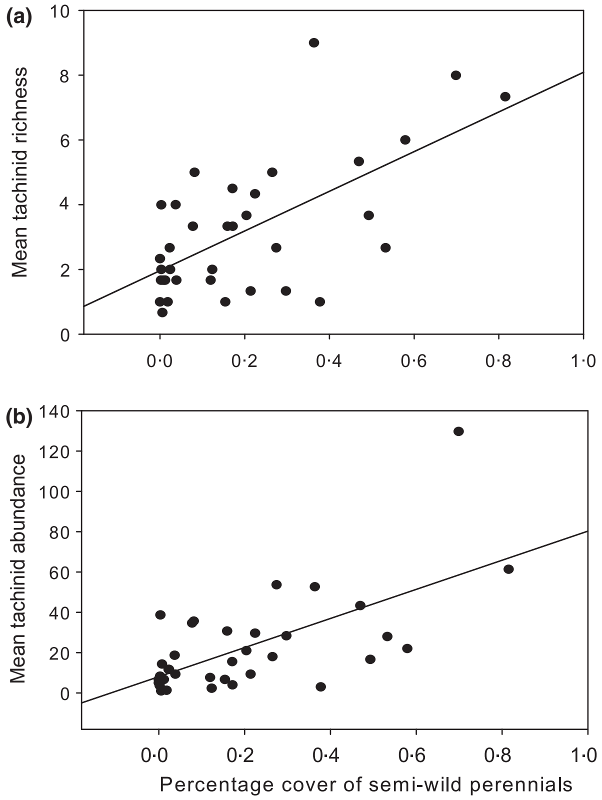

Fig. 3. Relationship between mean species richness of Malaise trapped tachinids in annual crop fields (a) and mean tachinid abundance (b) with the strongest predictor variable in the landscape (principal component 1) for both the 0·5-km landscape scale (shown) and the 1·5-km scale.

SENTINEL EXPERIMENTS

Mean parasitism of sentinel larvae by tachinid flies, expressed as a percentage of reared adults, was 6·7% in summer (range: 0–29% per field; 77% recovery of larvae from field) and 14·8% in autumn (range: 0–93%; 41% larval recovery) 2005. Ehler & Miller (1978) found high *T. ni* predation rates (50%) in fields without insecticides; thus, differential predator pressure may have accounted for a trend of higher sentinel disappearance in fields that had higher values of PC2 in autumn and crop diversity in both summer and autumn (Bothwell Allen and Letourneau, unpublished data). Six tachinid species (*Madremyia saundersii* Williston, *Voria ruralis, Lespesia archippivora* Riley, *Compsilura concinnata*, *Siphona plusiae* and *Eucelatoria armigera*) were reared from *T. ni* sentinel larvae after field exposure in autumn 2005. All of these species were represented in Malaise trap samples, with *S. plusiae* and *E. armigera* most abundant. However, *V. ruralis* and *M. saundersii* accounted for most of the tachinid parasitism of *T. ni* sentinels (approximately 35% and 40%, respectively). Relatively higher parasitism by *V. ruralis* than *S. plusiae* is consistent with previous studies of *T. ni* parasitism (Oatman 1966; Clancy 1969); given its relatively small size, *S. plusiae* could possibly prefer early instar larvae as hosts. Neither the total abundance of tachinids nor the abundance of the six species reared from *T. ni* was related to parasitism rates for the corresponding month. However, parasitism of sentinels by *M. saundersii* in autumn was positively correlated with the total abundance of *M. saundersii* captured in Malaise traps ($R^2 = 0{\cdot}13$, $P = 0{\cdot}0425$), and overall percentage parasitism in summer tended to be greater on farms with more *M. saundersii* ($R^2 = 0{\cdot}18$, $P = 0{\cdot}0780$). No such relationship was detected for *V. ruralis.*

Percentage parasitism of sentinel *T. ni* larvae showed no significant linear relationships with any of the landscape vegetation features associated with adult abundance and richness in Malaise traps, nor any of the principle components arising from combined landscape features. However, local polynomial regressions suggested the existence of threshold values of annual crop coverage in the summer and autumn experiments, above which tachinid parasitism strongly declined. These thresholds in autumn were 51% crop cover for all parasitism and *M. saundersii*, and 38% parasitism for *V. ruralis.* In each case, a simple step model (ANOVA) employing these thresholds explained more residual deviance with fewer parameters. Although overall parasitism did not exhibit a significant relationship with annual crop cover (Kruskal–Wallis test, $X^2 = 3{\cdot}24$, $P = 0{\cdot}072$), parasitism by both *V. ruralis* and *M. saundersii* was significantly greater on sentinels placed in fields with relatively low crop cover ($X^2 = 5{\cdot}01$, $P = 0{\cdot}025$ and $X^2 = 5{\cdot}27$, $P = 0{\cdot}022$, respectively; Fig. 4). Although high parasitism rates were also restricted to fields with low cover of annual crops in summer, we could not test for thresholds statistically because most of the 19 fields in the smaller summer sentinel larva trials happened to have less than 50% cover of annual cropland. The number of tachinid species emerging from sentinel *T. ni* larvae in the fall was negatively associated with the cover of annual crops in the landscape ($R^2 = 12{\cdot}6$, $P = 0{\cdot}0498$) and positively associated with in-field crop diversity ($R^2 = 26{\cdot}2$, $P = 0{\cdot}0033$).

Discussion

The positive association between semi-wild perennial vegetation cover around annual crop fields and the abundance and richness of tachinids visiting those fields is consistent with results for other natural enemies (Chaplin-Kramer *et al.* 2011), and supports our prediction that landscapes with persistent vegetation can augment the biodiversity of beneficial insects and potential for biological control services. The observation that spring and summer temporal communities exhibited a similar positive relationship with PC1 (high semi-wild perennial cover, low annual crop cover), along with positive effects of PC1 on tachinid diversity in spring and autumn, suggest that the relationship is robust. The absence of this pattern with generalist tachinid abundance in autumn but a significant increase in e^H could be due to the movement of species that can easily switch among habitats or hosts from non-agricultural habitats, highly desiccated after the dry California summer to irrigated annual crops. This interpretation is supported by the following observations: (i) abundance of specialized tachinids retained a strong negative association with annual crop cover during these times, (ii) tachinid richness and diversity exhibited a trend consistent among sampling times (i.e. positive influence of semi-wild perennial vegetation), (iii) sentinel caterpillars experienced higher rates of parasitism by generalist tachinids in autumn than in summer and (iv) annual crop cover was positively associated with generalist abundance in autumn.

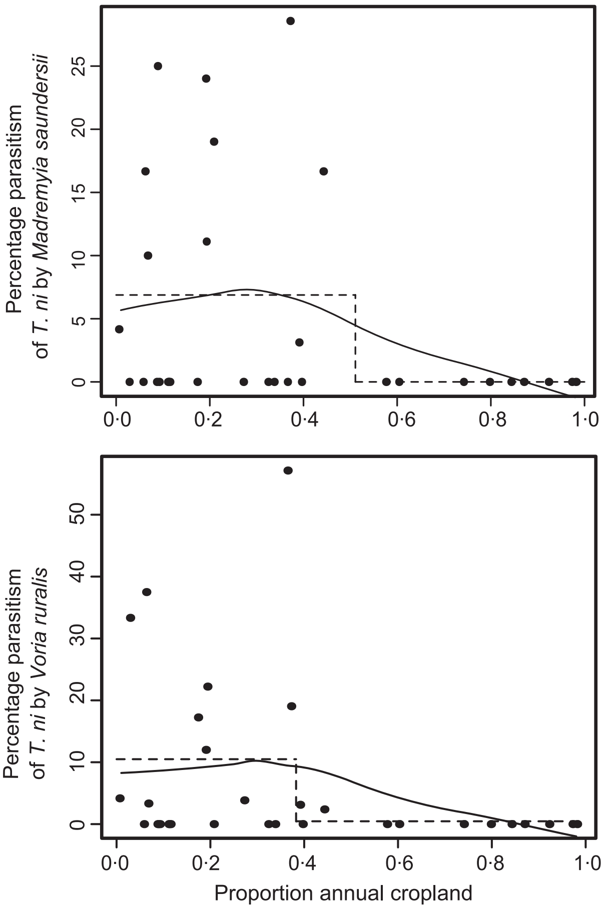

Fig. 4. Relationship of annual crop cover in the landscape (0·5 km) with the percentage parasitism of sentinel *Trichoplusia ni* larvae in autumn for *Madremyia saundersii* (top) and *Voria ruralis* (bottom). Solid curves are fitted local polynomial regression lines and dotted lines represent step models indicating mean parasitism above and below the threshold.

Each of the four most abundant tachinid species collected in traps is known to attack common pests of annual crops and is likely to have been parasitizing hosts in the farm fields where they were sampled. For example, the most abundant species, *Siphona plusiae* (1622 individuals), is primarily a parasitoid of alfalfa looper *Autographa californica* Speyer and *T. ni*, both generalist pests of many crops (Capinera 2001; Wold-Burkness *et al.* 2005). However, abundance of this tachinid followed the same trends as total tachinid richness – a positive association with surrounding perennial vegetation and a negative association with annual crop coverage. Although *S. plusiae* may frequently attack hosts in the farm environment, they may benefit from surrounding non-crop habitats due to the presence of alternate hosts (e.g. California Oakworm, *Phryganidia californica* Packard a persistent and occasionally outbreaking herbivore on oaks), adult resources [e.g. flowers (Tooker, Hauser & Hanks 2006)] and undisturbed pupation sites. The next two most abundant tachinid species, *Eucelatoria armigera* and *Periscepsia helymus*, are primarily parasitoids of noctuid moths including many serious pest species such as black cutworm *Agrotis ipsilon* Hufnagel, corn earworm *Heliothis zea* Boddie, armyworm *Pseudaletia unipuncta* Haworth, and fall armyworm *Spodoptera frugiperda* Smith. Interestingly, the fourth most abundant species, *Triarthria setipennis,* was intentionally introduced to the western United States for control of the European earwig *Forficula auricularia* L. (O'Hara 1996), which were commonly observed in some of the fields.

Some proportion of the tachinid taxa caught rarely in our traps are likely transients moving among non-crop habitats surrounding the fields (e.g. *Protodejeania echinata*

Thomson, a parasitoid of the western tussock moth *Orgyia vetusta* Boisduval Lymantriidae found on woody plants such as oaks, lupines and fruit trees in coastal California), but the majority of species recovered are likely to find at least some suitable host taxa in the farm environment (Appendix S2). As suggested for *S. plusiae*, less frequently disturbed, non-crop habitat is likely to provide a refuge for these other tachinids in terms of alternate hosts, adult resources and stable pupation sites (Landis, Wratten & Gurr 2000; Olson & Wackers 2007). The persistence of significant positive associations of richness and abundance of tachinids and cover of semi-wild perennials when *S. plusiae* is excluded from our samples strongly suggests that complex landscapes provide better 'insurance' over the course of contingencies associated with environmental variability (Hooper *et al.* 2005; Letourneau *et al.* 2009). That is, given some redundancy among species within a functional group, under conditions adverse to dominant species, herbivore suppression may be maintained by the presence of other species (Menalled *et al.* 2003).

Parasitism rates of sentinel larvae averaged from 2% to 15% of individuals recovered from field exposure, with over 60% parasitized at some sites. These estimates are conservative, as larvae that died of other causes may have been parasitized, and parasitism frequencies were achieved with limited exposure (1 week) of the sentinels to parasitoids. Thus, tachinids have the potential to cause significant mortality of agricultural pests in these annual crop fields. However, a recent meta-analysis (Chaplin-Kramer *et al.* 2011) identified few studies that demonstrate enhanced biological control from prominent landscape effects on parasitoid abundance and richness. Although linear relationships between landscape (e.g. PC1) and tachinid richness and abundance were not evident with parasitism rates of sentinels, landscape complexity may have had a nonlinear, threshold effect on mortality from tachinids as most sentinel parasitism occurred in crop fields with less than 51% annual crop cover. Interestingly, the pattern of parasitism rates for *T. ni* suggested different landscape complexity thresholds for parasitism by the two most important tachinid species. The negative association between tachinid species richness in Malaise traps and cover of annual crops was reflected in the number of tachinid species emerging from sentinel *T. ni* larvae and crop cover.

A positive association between number of tachinid species emerging from sentinel larvae and in-field crop diversity is consistent with studies that have found a beneficial effect of intercropping and weedy crops, supporting higher numbers of tachinids in crops (Abate 1991). In contrast, Olson & Wackers (2007) showed that increased tachinid abundance was often restricted to the field margins established around cotton, which may have acted as a parasitoid sink rather than a source. Marino *et al.* (2006) argued that because most parasitoids of pest Lepidoptera are generalists whose alternative hosts tend to be associated with late successional habitats, agricultural environments containing more of these late successional habitats should possess higher richness and abundance of parasitoids. The strong positive associations of tachinid abundance and richness with non-crop perennial vegetation, and the negative relationship with annual crop area in this study, support the conclusions of Marino *et al.* (2006) that 'effective conservation of native parasitoids will probably require the preservation and/or restoration of late successional habitats within the agricultural landscape'.

The growing body of research on ecosystem services worldwide supports land-managers and policy-makers who take the long view of agroecosystem management for sustainable agriculture and move toward stemming or reversing rates of cropland intensification. Managing landscape complexity and biodiversity for their beneficial contributions is critical for reducing pesticide contamination through enhanced biological control and central to the redesign of agroecosystems for reduced vulnerability to pests (Letourneau 2012). Thus, new protocols suggesting removal of wildlife habitat fragments around farms in hopes of reducing microbial food contamination events should be re-examined as counterproductive for biodiversity conservation (Sutherland *et al.* 2012), weighing the added value of these refugia for biological control agents in ephemeral crops. The applications of ecological research in agriculture are foundational for the integrated science and policy needed to transform food production systems to support global food security, public health and functional environments.

Acknowledgements

Funding from USDA-NRI grant 2005-55302-16345 and 25 organic vegetable growers made this study possible. We thank Brian Fulfrost, Joann Heraty and Hilary Devlin for excellent GIS training and support, specimen sorting, and sorting and identification, respectively.

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Received 31 January 2012; accepted 21 September 2012
Handling Editor: Owen Lewis

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. The 1.5 km radius landscape variable loadings on PCA axes 1–7 and the percentage variance explained by each principal component, by the percent cover of semi-wild annual and perennial vegetation, annual crops, conifers, coyote brush, *Eucalyptus*, suburban residential buildings and yards, isolated rural buildings and yards, oak woodlands, perennial crops, riparian and marsh, sage brush, and wild vegetation richness. Variables with strong loadings are indicated in bold. Note that in this analysis PC1 has negative loadings for semi-wild perennial vegetation and positive loadings for annual crop, in contrast to the 0.5 km scale analysis (the signs of these loadings are essentially arbitrary).

Table S2. Tachinid species collected with Malaise traps in organic farms in 2005 and 2006. M, J, and S indicate the number of specimens collected in sample in May 2006, July 2005, and September 2005.

Table S3. A summary of generalized linear models selected by AIC for analyses employing principal components (left) and specific landscape variables (right) at the large, 1.5 km scale. Significant P-values after Holm's sequential Bonferroni correction for each data set are indicated in bold. See Table S1 for explanations of variable abbreviations.