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Relative Densities of Natural Enemy and Pest Insects Within California Hedgerows

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ABSTRACT   Research on hedgerow design for supporting communities of natural enemies for biological control lags behind farmer innovation in California, where assemblages of perennial plant species have been used on crop field margins in the last decade. We compared natural enemy to pest ratios between fields with hedgerows and fields with weedy margins by sampling beneficial insects and key pests of vegetables on sticky cards. We used biweekly vacuum samples to measure the distribution of key insect taxa among native perennial plant species with respect to the timing and intensity of bloom. Sticky cards indicated a trend that field margins with hedgerows support a higher ratio of natural enemies to pests compared with weedy borders. Hedgerow plant species hosted different relative densities of a generally overlapping insect community, and the timing and intensity of bloom only explained a small proportion of the variation in insect abundance at plant species and among hedgerows, with the exception of *Orius* spp. on *Achillea millefolium* L. and *Baccharis pilularis* De Candolle. Indicator Species Analysis showed an affinity of parasitic wasps, especially in the super-family Chalcidoidea, for *B. pilularis* whether or not it was in flower. *A. millefolium* was attractive to predatory and herbivorous homopterans; *Heteromeles arbutifolia* (Lindley) Roemer and *B. pilularis* to *Diabrotica undecimpunctata undecimpunctata* Mannerheim; and *Rhamnus californica* Eschsch to Hemerobiidae. Perennial hedgerows can be designed through species selection to support particular beneficial insect taxa, but plant resources beyond floral availability may be critical in providing structural refuges, alternative prey, and other attractive qualities that are often overlooked.

KEY WORDS   hedgerow, conservation biological control, biodiversity, natural enemy, insectary plant

Conservation biological control (CBC) aims to increase the abundance of resident natural enemies of insect pests by reducing mortality events and creating habitat that provides pollen, nectar, alternative prey, a favorable microclimate, and shelter for overwintering (Ehler 1998, Landis et al. 2000). Annual and semi-annual crop systems are particularly challenging environments for conservation biological control because the high frequency and intensity of tillage and pesticide applications disrupt arthropod community development (Ehler and Miller 1978, Letourneau 1998) and reduce floral resources (Heimpel and Jervis 2005). Nectar fuels host searching and increases longevity and fecundity in female wasps (Idris and Grafius 1995, Baggen and Gurr 1998, Johanowicz and Mitchell 2000, Costamanga and Landis 2004, Berndt and Wratten 2005), and can shift the sex ratio toward females in some parasitoids (Berndt and Wratten 2005). Protein from pollen can increase survivorship and reproduction of predators (Cowgill et al. 1993). However, natural enemies may prefer some flowers over others because of the viscosity or ratio of different sugars in the nectar (Baker and Baker 1986, Koptur 2005), type of pollen (Haslett 1989, Cowgill et al. 1993, Tooker et al. 2006, Hogg et al. 2011), or their physical ability to access and collect these resources from the flower (Idris and Grafius 1995, Koptur 2005, Olson et al. 2005, Sivinski et al. 2011). In practice, floral resource provisioning for beneficial insects in annual crops has relied on planting insectaries of annual exotic forbs, such as sweet alyssum (*Lobularia maritima* L. Desvaux), buckwheat (*Fagopyrum esculentum* Moench), and coriander (*Coriandrum sativum* L.) (Baggen and Gurr 1998, Chaney 1998, Colley and Luna 2000, Johanowicz and Mitchell 2000, Spellman et al. 2006, Irvin and Hoddle 2007, Lee and Heimpel 2008), at intervals in fields managed using existing technology and cultivation practices. Perennial plants in contrast, require dedicated land, but the permanent vegetative cover they provide may be suitable for overwintering (Dennis and Fry 1992), has architectural complexity, and provides shelter from agricultural disturbance or environmental extremes, as well as alternative prey, nectar, and pollen (Landis et al. 2000, Bianchi et al. 2006). Native perennials can also enhance local biodiversity, be better adapted to the local environment (see Fiedler and Landis 2007, Frank

et al. 2008), allow for early dispersal of natural enemies into crop fields to regulate crop pests, and thus compensate for disturbances in annual crop areas (Letourneau 1998). Although hedgerows have a long history in Europe (van Emden 1965, Pollard 1971, Charrier 1997, Burel et al. 1998, Paoletti et al. 1997, Baudry et al. 2000), in the United States they have been screened less than annual plants for CBC habitat because of the time needed for establishment.

In coastal California, where the climate is mild and land prices are high, growers maximize yield by rotating two to three short-cycle vegetable crops from March through November and when feasible, follow with a winter cover crop to restore soil fertility and prevent erosion. In response to the disturbance caused by intensive crop rotation, alternating deep tillage bed preparation and shallow in-row cultivations to control weeds with brief periods of bare ground fallow, some growers have established native perennial hedgerows in vegetable, strawberry, and orchard systems as beneficial habitat for insects, but also as windbreaks, for soil conservation, and weed suppression (Bugg et al. 1998, T.L.P.G., unpublished data). Linear hedgerows measuring 3–5 m wide and running hundreds of meters along field edges typically contain assemblages of 10–40 species of native shrubs, small trees, grasses, and forbs (see Earnshaw 2004 for a complete list). Plant species selection has been based on establishing an architecturally complex and primarily native assemblage of flowering plants with staggered bloom periods for attracting and retaining insect natural enemies on the farm. While diversifying the agricultural mosaic with species-rich hedgerows may increase the opportunities for natural enemy establishment and regulation of crop pests, successful CBC depends on adding the right elements of diversity, not more plant species per se (Landis et al. 2000, Wäckers 2004, Bianchi et al. 2006, Tscharntke et al. 2007). For example, insect pests also use food resources provided by noncrop plants (Baggen and Gurr 1998, Forehand et al. 2006, Lavandero et al. 2006) and may overwinter in seminatural habitats (Pollard 1971, Altieri and Letourneau 1984, Bugg et al. 1998, Bugg and Pickett 1998). Herbivore populations may also increase if floral subsidies enhance processes at the fourth tropic level, resulting in a disruption of a trophic cascade (Straub et al. 2008). Though CBC plant selection aims to minimize the potential for exacerbating pest damage on the crop, some herbivore presence in hedgerows is potentially desirable when they support specialist natural enemy populations.

Ideally, plants are screened for insectary quality before they are incorporated into farm design. However, because Central Coast growers are already establishing hedgerows, they provide a particularly robust testing ground for assessing, in a commercial agriculture context, their function as beneficial insect habitat. The overall purpose of this study was to assess the habitat quality of hedgerows for insect natural enemies and pests important to Central Coast vegetable systems. We used on-farm sampling to compare the relative densities of predators, parasitoids, and key herbivore pests on field margins with and without hedgerows established by growers in California's Central Coast region, and to compare the insect fauna associated with six species of native perennials as well as the impact of floral resource availability on these associations.

Materials and Methods

We conducted this study in 2005 and 2006 at four organic vegetable farms with bordering hedgerows in the northern region of the Central Coast of California. California's Central Coast has a Mediterranean climate with cool, foggy summers along the coast and warm summers inland. Most of the rainfall occurs between November and April. Two coastal sites in Watsonville, Santa Cruz County (36° 54′37″ N/121° 45′20″ W) had mean daily summer temperatures of 16–17°C and 584 mm mean annual precipitation (National Oceanic and Atmospheric Administration [NOAA] 2000). For two inland sites in San Benito County (36° 44′44″ N/121° 17′19″ W), the temperature was 19–23°C with 432 mm rainfall (NOAA 2000). Mixed vegetables and lettuce are the top two commodities produced in both counties, with production fields covering over 265 km^2 (U.S. Department of Agriculture [USDA] 2007), an increasing proportion of which are under organic management (California Certified Organic Farmers [CCOF] 2007). Surrounding vegetation types include grasslands, chaparral, mixed woodlands, and wetlands. From 20 hedgerows sites evaluated in 2003, we selected four farms that had hedgerows that were at least 2 yr old, were under organic management to reduce the influence of insecticides, had a similar crop matrix, included several of the most common hedgerow plant species, and were upwind of the crop fields (Table 1).

Field Margin Comparison of Natural Enemy to Pest Ratios. To measure the effect of hedgerows on the relative abundances of natural enemies and pests within crop fields, on 2 August and 6 September 2005 we haphazardly placed five yellow sticky cards at 0, 50, and 100 m from two hedgerows and two weedy field margins (15 traps per field). Traps were collected after 3 d. We chose Watsonville site two and the Hollister hedgerow because each had a nearby control field with similar vegetable matrix and organic management. The control field for the Hollister hedgerow was at the same location, >200 m away, while the control field for the Watsonville site was approximately three miles away and similarly along the coast. The Watsonville control field was tilled in between trials, thus for the second trial we selected another control field, which was also an organic vegetable field about three miles away. We counted insect natural enemies and pests on each trap and pooled the abundance of the five traps for a total abundance per distance per site. Natural enemies included *Hippodamia convergens* Guerin–Meneville (Coleoptera: Coccinellidae), Syrphidae (Diptera), Tachinidae (Diptera), *Nabis* spp. (Hemiptera: Nabidae), *Orius* spp. (Hemiptera: Anthocoridae), *Geocoris* spp. (Hemiptera: Lygaeidae), Ichneu-

Table 1. Descriptions of four hedgerows on organic vegetable farms on California's Central Coast sampled for insect natural enemies and pests in 2005 and 2006

Hedgerow characteristics	Watsonville site 1	Watsonville site 2	San Juan Bautista	Hollister
Crops in adjacent field	Cole crops, cucurbits, lettuce, onions, flowers	Salad greens	Cole crops, cucurbits, lettuce, onions, leeks	Cucurbits, peppers, onions, leeks
Established	2002	2000	1999	2001
Linear direction	NE−SE	E−W	N−S	N−S
Wind direction	W E	SW NE	W E	W E
Length (m)	150	972	366	318
Width (m)	4	3	3	3
Plants sampled	A. millefolium	A. millefolium	A. millefolium	A. millefolium
	B. pilularis	B. pilularis	B. pilularis	B. pilularis
	C. griseus	C. griseus	C. griseus	C. Ray Hartman
	C. Ray Hartman	C. Ray Hartman	C. Ray Hartman	H. arbutifolia
	E. giganteum	H. arbutifolia	E. giganteum	R. californica
	R. californica	R. californica	H. arbutifolia	
			R. californica	
Plant species richness	35	15	17	15
% Gaps	31–50%	<10%	10–30%	10–30%

% Gaps is the percentage of the length of the hedgerow that did not have perennial plant cover, because of die-off of shrubs, measured in 2003.

monidae (Hymenoptera), Braconidae (Hymenoptera), and Chalcidoidea (Hymenoptera). Pests were spotted cucumber beetles, *Diabrotica undecimpunctata undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae); striped cucumber beetles, *Acalymma trivittatum* Mannerheim (Coleoptera: Chrysomelidae); western tarnished plant bug, *Lygus hesperus* Knight (Hemiptera: Lygaeidae); and all aphids (Homoptera: Aphididae).

Hedgerow Plant Species Selection. Common yarrow, *Achillea millefolium* L. (Family Asteraceae); coyote brush, *Baccharis pilularis* DeCandolle (Family, Asteraceae); California lilac, *Ceanothus griseus* (Trelease) McMinn (Family, Rhamnaceae); perennial buckwheat, *Eriogonum giganteum* Sereno Watson (Family, Polgonaceae); toyon, *Heteromeles arbutifolia* (Lindley) Roemer (Family, Rosaceae); and coffee-berry, *Rhamnus californica* Eschsch (Family Rhamnaceae) are foundational plant species used in hedgerow design and were most frequently represented in our 2003 survey of Central Coast hedgerows. These native species provide pollen and nectar to insects, have overlapping bloom periods (Table 2) and are well adapted to California's northern Central Coast climate (Earnshaw 2004). In 2006, we also sampled on the hybrid variety *C. arboreus* × *C. griseus* 'Ray Hartman,' which blooms a week or two later than *C. griseus* and has a second minor bloom period in the late summer. *H. arbutifolia* was represented at three sites and *E. giganteum* at two sites.

Sampling Methods. To sample hedgerow plant species for key insect abundance and bloom intensity, in 2005, we marked four or five stratified random points

Table 2. Bloom period of plant species included in the study

Common name	Scientific name	Plant family	Ave (±SD) floral area at peak bloom (m²)	Bloom period in study region											
				Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
California lilac	*Ceanothus griseus*	Rhamnaceae	1.3 (±2.1)		○	○	●	○	○						
California lilac	*Ceanothus* Ray Hartman	Rhamnaceae	0.69 (±0.68)			○	○	●	○				○		
Coffeeberry	*Rhamnus californica*	Rhamnaceae	0.16 (±0.15)				○	●	○			○			
Common yarrow	*Achillea millefolium*	Asteraceae	0.79 (±0.68)				○	○	●	○	○				
Toyon	*Heteromeles arbutifolia*	Rosaceae	0.96 (±0.76)						○	○	●	○			
Perennial buckwheat	*Eriogonum giganteum*	Polygonaceae	1.5 (±0.98)						○	○	●	○			
Coyote brush	*Baccharis pilularis*	Asteraceae	2.02 (±1.6)									○	●	○	○

○ Open flowers may be present
● Peak bloom

The plant data from the April to Oct., which include the peak bloom periods, are based on observations and measurements taken at the four hedgerow sites. Plant data from Feb., Mar., Nov., and Dec. are based on observations of these plants in northern California presented in Earnshaw (2004).

along each hedgerow, depending on the length of the hedgerow, and selected the nearest individual of each plant species. Diseased or dying plants were excluded from selection. In 2005, we measured the proportion of each plant's floral canopy in bloom (% bloom) by counting the number of open flowers in relation to closed buds on several flower heads and averaging the values for each individual plant (Andow and Risch 1985). Because % bloom was not comparable among plant species, in 2006 we measured the area of blooming flowers on the vacuumed plant individual. Using a 1 m^2-grid, we measured the proportion of the plant cover in flower heads and then subsampled four flower heads and averaged the proportion of blooming flowers. We calculated the floral resource area sampled (square centimeters) as the surface area of plant sampled with the vacuum multiplied by the percentage of that area with flower heads multiplied by the percentage of those flowers that were in bloom. Also in 2006, temperature was recorded hourly throughout the season with Onset Hobo temperature dataloggers.

We sampled insect taxa at the plant individuals eight times in 2005 and nine times in 2006 between the months of May and October. We vacuum-sampled hedgerow plants (Osborne and Allen 1999), a standard method for sampling arthropods on coastal sage scrub vegetation (Buffington and Redak 1998). The vacuum was moved continuously through the canopy of each plant for the same amount of time (30 s in 2005, 60 s in 2006) on the lee side of the hedgerow between 10 a.m. and 3 p.m., when temperatures were above 15°C. Insects killed with ethyl acetate were stored frozen, and identified using Borror et al. (1989) and Goulet and Huber (1993). We identified parasitoids as Tachinidae (Diptera) or Hymenoptera in 2005, and separated parasitoids as Tachinidae, Braconidae, Ichneumonidae, Chalcidoidea, and Cynipoidea in 2006. The predatory taxa we monitored included Coccinellidae, Syrphidae, Chrysopidae, Hemerobiidae, and the genera *Nabis* spp., *Orius* spp., and *Geocoris* spp.. We counted aphids and four species of insect pests, *D. undecimpunctata undecimpunctata, A. trivittatum, Phyllotreta pusilla* Horn (Coleoptera: Chrysomelidae) (2006 only), and *L. hesperus* as indicators of potential negative effects of hedgerow plants. *L. hesperus* is not a key pest in vegetable systems, and may even function as an opportunistic predator (Chang and Snyder 2004); however, tarnished plant bugs cause cat-facing damage to strawberries, a crop that is often rotated with vegetables. We selected key taxa a priori from the University of California Integrated Pest Management online guidelines for vegetable production (University of California Integrated Pest Management [UC IPM] 2012) to represent an array of important herbivores and carnivores in mixed vegetable systems (Ehler and van den Bosch 1974, Flint and Dreistadt 1998, Myers 1998, Ehler 2004). Taxa range in length from 1 to 9 mm with various morphological features that influence their ability to access different plant resources, and particular nutritional requirements that could lead to selectivity for different plant species (Bugg 1990). Documented observations suggest that

many of these insect groups are attracted to particular plant families or species (Jervis et al. 1993, Colley and Luna 2000, Wäckers 2004, Tooker et al. 2006, Hogg et al. 2011, Sivinski et al. 2011).

Data Analysis. We combined the two sticky card sampling dates and used Kruskal–Wallis tests with SAS/STAT software version 9.2 (SAS Institute 2009) to compare natural enemy to pest ratios at different distances within vegetable fields with hedgerows and vegetable fields with weedy margins ($n = 4$).

We used Multi-Response Permutation Procedures (MRPP) in PC-ORD v.5 (McCune and Mefford 2006), a nonparametric distance-based method that does not require a balanced design, to test the hypothesis of no difference in the composition of insect taxa among plant species, hedgerows, and sampling times (Zimmerman et al. 1985). Sørensen (1948) distances on insect abundance and plant groups were weighted by $n/\text{sum}(n)$. MRPP does not require linear species responses of insect abundances or normally distributed errors. Therefore, it allows for testing despite large differences in the distributions and occurrences of insect taxa among vacuum samples. To characterize insect abundance per plant species, we averaged the number of insects collected in each insect taxon from individual plant replicates at each site on each sampling date. Nontransformed mean abundances of insect taxa were relativized within each insect taxon. MRPP produces three statistics that are useful for comparing insect taxa composition between *a priori* groups: "T" that describes the separation between groups (the more negative the value, the greater the separation), the agreement statistic "A" that describes within group homogeneity (a measure of effect size), and a *P* value that shows the likelihood of getting a δ (the weighted mean within-group distance) as extreme or more extreme than the observed δ given the distribution of possible δ (McCune and Grace 2002). Multiple comparisons, using a Sørensen distance measure and a Bonferroni correction, indicated where differences in taxa composition occurred among hedgerow plant species and hedgerow sites.

To determine the differences in occurrence of specific insect taxa among hedgerow plant species, we used Indicator Species Analysis (Dufrêne and Legendre 1997), a complementary procedure to MRPP (McCune and Grace 2002). An indicator value (IV) for an insect taxon associated with a hedgerow plant species, which ranges between 0 and 100, is the product of the insect species' relative abundance and relative frequency at that plant species. An insect taxon that is a perfect indicator (IV = 100) of a hedgerow plant species would always be present on that species and be exclusive to that species (i.e., not occur at the other plant species). High IVs for an insect taxon thus depend on having both a high relative abundance and high relative frequency on one plant species in comparison to the other plant species. Statistical significance for the maximum IV among groups was determined with a Monte Carlo randomization procedure. The *P* value represents the probability of achieving the

same or higher IV given the taxon's distribution of abundance.

For insect taxa that showed faithfulness to particular plant species, we tested the hypothesis that the insect–plant association was related to floral resource availability of the plant by conducting linear regressions using JMP 9.0. We used insect abundance per vacuum sample from each plant replicate at each site over time and floral resource availability of the plant at the time of insect sampling. Insect abundance data were transformed using the formula $Log_{10} (x + 1)$.

To descriptively evaluate trends in insect composition between hedgerow sites, we performed nonmetric multidimensional scaling (NMS) (PC-ORD v. 5) on the same matrices used for MRPP and Indicator Species Analysis, where a plot represents the average individual for a given plant species at a particular site and sample period. Hedgerow site was overlaid on the NMS ordinations. We used joint plots to simultaneously evaluate available environmental variables (average day time temperature, average night time temperature, temperature at time of sampling, floral resource availability, and time). The angle and length of the vector on the joint plot indicates the direction and strength of the relationship between the variable and the ordination (McCune and Grace 2002). Because NMS is done with a random number seed, generating a unique graph with each analysis, we ran multiple analyses to examine consistency in the results and chose the configuration that best illustrated the trends in the insect data. Both the 2005 and 2006 matrix produced consistent, interpretable, and significant three-dimensional solutions. For both matrices, the final stress, a measure of the departure of the NMS ordination from the original data, was 21, which is reasonable given the high number of sample units in both matrices (151 and 223, respectively) and the inclusion of rare insect taxa, both of which produce solutions with high final stress (McCune and Grace 2002). Most ecological community data produce solutions with stress between 10 and 20 (McCune and Grace 2002).

Results

Perennial hedgerows established by vegetable growers had an insect natural enemy to pest ratio of 29.7 ± 16.2 SE compared with 5.6 ± 2.8 SE in weedy field margins in 2005; however, the difference was not significant (Kruskal–Wallis test; $n = 4$; $P > 0.05$). Ratios within the fields at 50 and 100 m were similar between treatments (Fig. 1).

Of over 40,000 insects vacuum-collected within the key taxa, a mean of 13.6 ± 0.8 SE were natural enemies per 30 s sample in 2005 and 23.1 ± 1.2 SE per 60 s sample in 2006. Relative abundances among taxa were consistent over the two seasons (Table 3; Pearson's coefficient; $R^2 > 0.75$; $P < 0.0001$). *Orius* spp. was the most abundant and common predator present in over 20% of all vacuum samples in both years. The spotted cucumber beetle, *D. undecimpunctata undecimpuntacta,* was almost as abundant as minute pirate bugs,
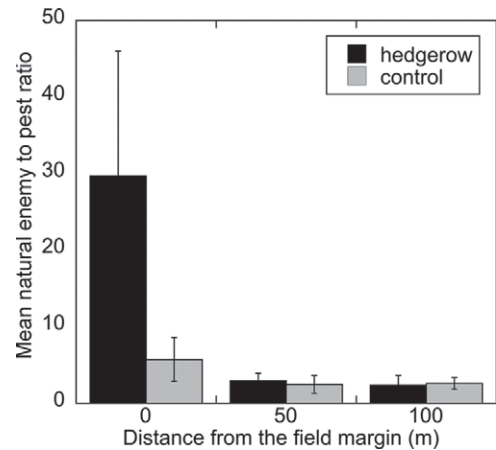

Fig. 1. Mean natural enemy to pest ratios at three distances into organic vegetable fields bordered with a hedgerow and control fields bordered with weeds ($n = 4$). Data were collected in August and September of 2005 in Watsonville and Hollister, CA.

Orius spp., totaling over 3,500 individuals. However, the highest abundances of this pest on hedgerow plants, representing 60% of all *D. undecimpunctata undecimpuntacta* collected in 2006, were at one of the inland sites. The overall average natural enemy to pest ratio was 11.4 in 2005 and 15.2 in 2006. Coyote brush, *B. pilularis,* showed the greatest natural enemy to pest ratios (28.7 in 2005, 42.6 in 2006), compared with toyon, *H. arbutifolia,* with the lowest ratio (3.8 natural enemies per pest) in 2005 and buckwheat, *E. giganteum* lowest in 2006 with a ratio of 5.8. *B. pilularis* supported the greatest number of parasitoids in both years, and the greatest number of predators and herbivores in 2006 (Fig. 2). *A. millefolium* was attractive to predators in both years and to herbivores in 2005 (Fig. 2).

Seasonal Distribution of Insect Taxa. Insect community composition changed significantly over the growing season (MRPP; $P < 0.05$) as common taxa oscillated independently at all sites (Fig. 3). Parasitic Hymenoptera tended to be most abundant in May or June samples and had similar abundance patterns among hedgerows in 2006 (Fig. 3B). Inland hedgerows had higher peak abundances of *Orius* spp. especially in early summer and fall (Fig. 3C and D). *D. undecimpunctata undecimpunctata* abundance was an order of magnitude greater on one of the inland hedgerows where it peaked early in 2005 and late in 2006 (Fig. 3E and F). A consistently high number of natural enemies were collected from *B. pilularis* despite the time of season, with 31.6, 29.2, and 37.7 natural enemies per 30 s sample (2005) and 68.7, 56.6, and 71.1 per 60 s sample (2006) in the early season (mid-May to late June), mid-season (early July to mid-August), and late season (late August to mid-October), respectively.

Composition of Key Insect Taxa Among Plant Species. As predicted, the composition of key insect taxa differed between hedgerow plant species (Table 4). A perMANOVA analysis on a balanced matrix (achieved

Table 3. Summary of the total abundance and frequency (percentage of total individual vacuum samples) of key taxa in vacuum samples taken from hedgerow plants at four sites in 2005 and 2006

Order	Taxa	2005		2006	
		Total	Percent	Total	Percent
Coleoptera	*Acalymma trivittatum* Mannerheim	81	6	609	9
	Diabrotica undecimpunctata undecimpuntata Mannerheim	773	23	2,786	24
	Hippodamia convergens Guerin-Meneville	34	2	48	4
	Coccinellidae (Other)	25	2	637	20
	Phyllotreta pusilla Horn	—[a]	—	246	11
Diptera	Syrphidae	20	2	49	4
	Tachinidae	223	16	96	5
Hemiptera	*Geocoris* spp.	69	4	63	3
	Lygus hesperus Knight	94	7	65	3
	Nabis spp.	22	3	8	1
	Orius spp.	1,026	21	2,996	26
Homoptera	Aphidae	376	8	3,128	16
Hymenoptera	Parasitic Hymenoptera	7,699	85	19,712	89
	Braconidae	—	—	3,512	56
	Chalcidoidea	—	—	14,563	81
	Cynipoidea	—	—	561	23
	Ichneumonidae	—	—	1,076	31
Neuroptera	Chrysopidae	43	5	201	13
	Hemerobiidae	23	3	110	8
Total		10,508	73	30,754	

Larvae of Hemerobiidae, Chrysopidae, and Coccinellidae and nymphs of *Geocoris* spp., *Lygus hesperus*, and *Nabis* spp. are included in totals, although over 75% of individuals were adults. Parasitic Hymenoptera were not sorted to family level in 2005.

[a] An emdash indicates that taxa were not counted in that sampling year.

by removing data) showed that hedgerow plant species accounted for 15.5% ($F = 3.93$; df = 5; $P = 0.0002$) and 14% ($F = 5.41$; df = 6; $P = 0.0002$) of the variation in the relative abundance and frequency of the insect taxa in 2005 and 2006 respectively. The insect community collected on *A. millefolium* was significantly different from other plant species, especially *B. pilularis* (T statistic >12), in both years, and insect
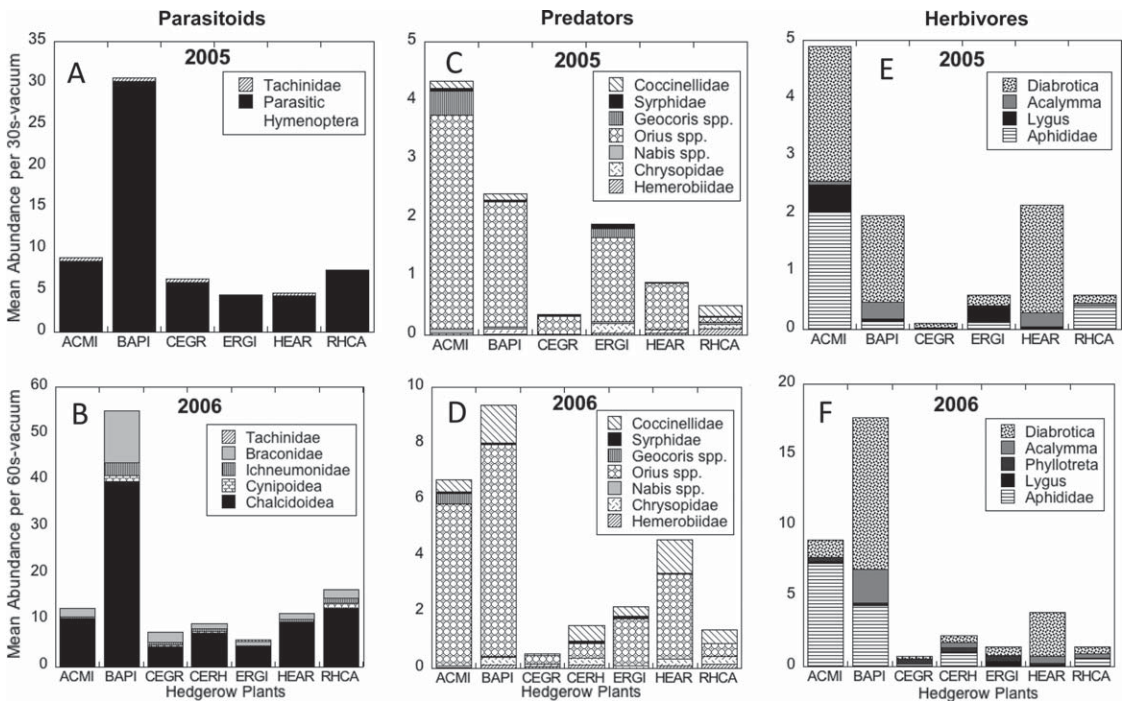

Fig. 2. Mean abundance of focal parasitoids (A and B), predators (C and D), and pest herbivores (E and F) collected at hedgerow plants in 2005 and 2006. Plants are *Achillea millefolium* L. (ACMI), *Baccharis pilularis* DC (BAPI), *Ceanothus griseus* (Trel.) McMinn (CEGR), *Ceanothus* 'Ray Hartman' (CERH), *Eriogonum giganteum* S. Watson (ERGI), *Heteromeles arbutifolia* Lindley (Roemer) (HEAR), and *Rhamnus californica* Eschsch (RHCA).
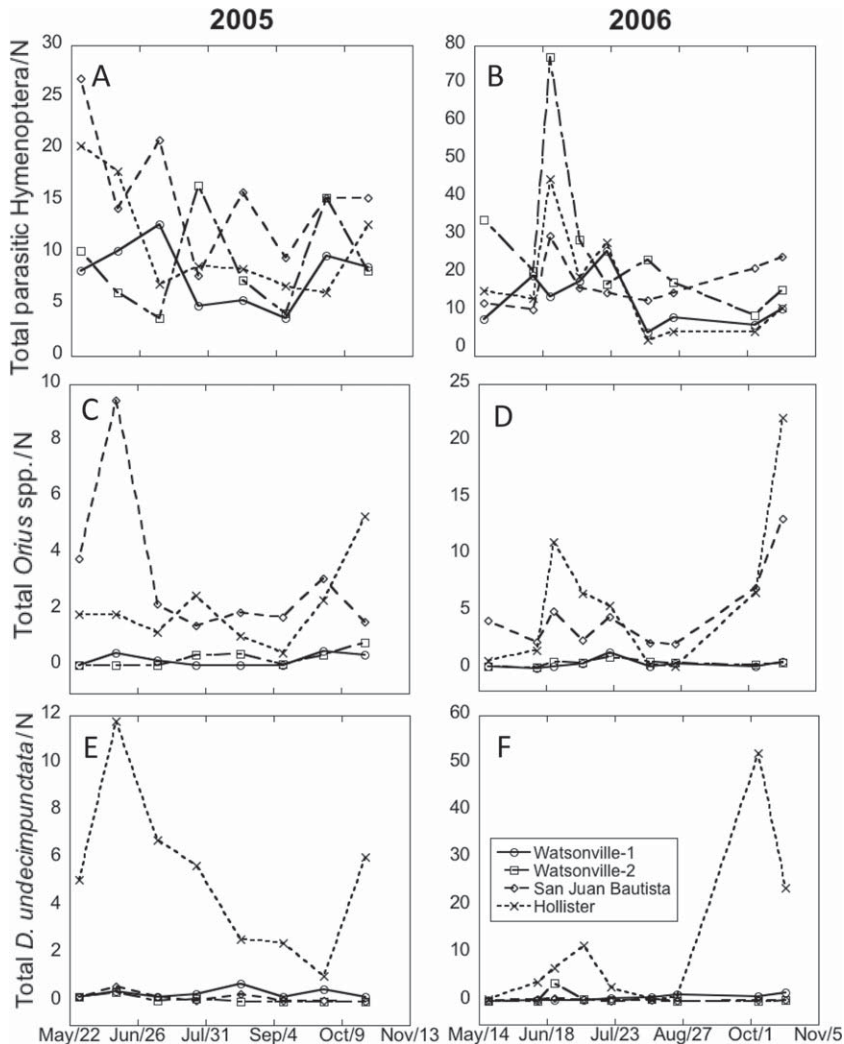
Fig. 3. Seasonal distribution of parasitic Hymenoptera (A and B), *Orius* spp. (C and D), and *D. undecimpunctata undecimpunctata* (E and F) per vacuum sample at four hedgerow sites in the Central Coast of California in 2005 and 2006.

composition at *B. pilularis* was significantly different from *C. griseus* and *E. giganteum.* Pairs of plant species that showed similar insect composition were *R. californica* and *H. arbutifolia* and *C. griseus* and *H. arbutifolia.*

Indicator Species Analyses identified some of the distinctions among hedgerow plant species (Tables 5 and 6). Parasitic Hymenoptera were highly characteristic of *B. pilularis* in 2005 (IV = 46; $P < 0.001$). In 2006, Chalcidoidea, Braconidae, Ichneumonidae, and Cynipoidea all showed significantly higher fidelity to *B. pilularis* than to other plant species (IVs >30; $P < 0.001$). Coccinellidae was also an indicator of *B. pilularis* in 2006. Syrphidae was a weak indicator taxon for *E. giganteum* only in 2006. The predatory bugs, *Geocoris* spp. were an indicator genus for *A. millefolium* in both years. In 2005, *Orius* spp. was also an indicator genus for *A. millefolium;* however, in 2006, *Orius* was equally indicative of *A. millefolium* as it was of *B. pilularis.* Of the

two lacewing taxa, only Hemerobiidae showed an association with a particular plant species, *R. californica,* and the relationship was apparent in both years.

Pest species were also associated with particular hedgerow plant species. Aphididae was characteristic of *A. millefolium* in 2005 and 2006. *L. hesperus* was associated with *A. millefolium* and *E. giganteum* in 2005 and to a high degree with *E. giganteum* in 2006. In 2005, *D. undecimpunctata undecimpunctata* was a weakly significant indicator of *A. millefolium,* while in 2006, *D. undecimpunctata undecimpunctata* was a strong indicator of *B. pilularis. A. trivittatum* was also an indicator taxon for *B. pilularis* in 2006. There was little insect activity on *C. griseus* from May to October, with sampling beginning after the peak bloom period of *C. griseus.* We may have missed usage of this plant species by key insect groups such as syrphid flies, which were abundant on hybrid *C. arboreus* ×

Table 4. Summary statistics for MRPP of 2005 and 2006 key insect abundance matrices using Sørensen distance measure

Factor	2005			2006		
	T statistic	A	P value	T statistic	A	P value
Plant	−17.65	0.064	0.0000*	−26.83	0.063	0.0000*
Time	−2.64	0.011	0.0080*	−11.73	0.032	0.0000*
Hedgerow	−15.65	0.044	0.0000*	−29.83	0.049	0.0000*
Multiple comparisons (Sørensen)						
Plants						
A. millefolium vs B. pilularis	−12.83	0.048	0.0000*	−16.84	0.052	0.0000*
A. millefolium vs C. griseus	−11.77	0.064	0.0000*	−9.99	0.041	0.0000*
A. millefolium vs C. Ray Hartman	—	—	—	−6.89	0.022	0.0000*
A. millefolium vs E. giganteum	−1.19	0.006	0.1211	−5.20	0.018	0.0002*
A. millefolium vs H. arbutifolia	−8.23	0.034	0.0000*	−5.62	0.021	0.0001*
A. millefolium vs R. californica	−10.43	0.040	0.0000*	−13.38	0.044	0.0000*
B. pilularis vs C. griseus	−11.94	0.071	0.0000*	−21.16	0.080	0.0000*
B. pilularis vs C. 'Ray Hartman'	—	—	—	−13.32	0.043	0.0000*
B. pilularis vs E. giganteum	−10.63	0.057	0.0000*	−17.64	0.062	0.0000*
B. pilularis vs H. arbutifolia	−8.77	0.043	0.0000*	−11.92	0.043	0.0000*
B. pilularis vs R. californica	−8.05	0.037	0.0000*	−12.08	0.039	0.0000*
C. griseus vs C. 'Ray Hartman'	—	—	—	−7.66	0.030	0.0000*
C. griseus vs E. giganteum	−5.14	0.052	0.0005*	−17.05	0.078	0.0000*
C. griseus vs H. arbutifolia	−2.68	0.023	0.0179	−3.89	0.019	0.0025
C. griseus vs R. californica	−5.45	0.037	0.0002*	−8.82	0.036	0.0000*
C. Ray Hartman vs E. giganteum	—	—	—	−9.77	0.034	0.0000*
C. Ray Hartman vs H. arbutifolia	—	—	—	−2.25	0.008	0.0267
C. Ray Hartman vs R. californica	—	—	—	−4.26	0.014	0.0010*
E. giganteum vs H. arbutifolia	−3.20	0.023	0.0072	−10.23	0.040	0.0000*
E. giganteum vs R. californica	−6.60	0.039	0.0000*	−18.00	0.066	0.0000*
H. arbutifolia vs R. californica	−2.21	0.012	0.0310	−2.18	0.008	0.0317
Hedgerows						
Watsonville 1 vs Watsonville 2	−2.37	0.009	0.0232	−7.67	0.017	0.0000*
Watsonville 1 vs San Juan Bautista	−7.19	0.024	0.0000*	−10.22	0.019	0.0000*
Watsonville 1 vs Hollister	−10.65	0.042	0.0000*	−19.03	0.039	0.0000*
Watsonville 2 vs San Juan Bautista	−4.34	0.014	0.0011*	−15.79	0.032	0.0000*
Watsonville 2 vs Hollister	−13.93	0.050	0.0000*	−30.14	0.063	0.0000*
San Juan Bautista vs Hollister	−13.91	0.045	0.0000*	−16.18	0.291	0.0000*

More negative values of T indicate greater separation between groups, and A is a measure of effect size. Multiple comparisons of plants and hedgerows are also shown and significance determined with a Bonferroni correction (for plant comparisons, adjusted P value = 0.002, for hedgerow site comparisons, adjusted P value = 0.008).

An asterisk indicates significant difference in insect composition among groups. An emdash indicates that the comparison was not made in that sampling year.

C. griseus Ray Hartman, a variety that blooms for a longer time period.

Composition of Key Insect Taxa Among Hedgerows. The composition of insect taxa also differed among hedgerow sites (Table 4). Particularly noteworthy was the high degree of separation among sites in 2006 (T-statistic = −29). Watsonville hedgerows were most similar to each other in insect composition, while the Hollister hedgerow showed the most separation from the other sites.

Table 5. Results of 2005 Indicator Species Analysis

	A. millefolium	B. pilularis	C. griseus	E. giganteum	H. arbutifolia	R. californica	P value
Parasitoids							
Parasitic Hymenoptera	14	49	10	7	8	11	0.0002*
Tachinidae	8	10	13	5	7	3	0.6015
Generalist predators							
Coccinelidae	10	4	0	0	0	4	0.1974
Syrphidae	3	2	2	6	0	0	0.3437
Orius spp.	26	9	1	10	3	0	0.0138*
Geocoris spp.	29	0	0	7	0	0	0.0004*
Nabis spp.	13	4	0	1	0	1	0.0300*
Chrysopidae	1	4	0	7	3	5	0.6605
Hemerobiidae	0	1	0	2	2	13	0.0310*
Herbivore pests							
D. undecimpunctata undecimpunctata	26	15	0	1	17	1	0.0666
A. trivittatum	1	14	0	0	9	1	0.0840
L. hesperus	32	1	0	21	0	0	0.0020*
Aphididae	32	2	0	1	0	5	0.0030*

Indicator values, ranging between 0 and 100, are the product of the relative abundance and frequency of the insect taxa collected at the hedgerow plant. An asterisk indicates a significant difference (P value < 0.05) among IVs for plant groups.

Table 6. Results of 2006 Indicator Species Analysis

	A. millefolium	B. pilularis	C. griseus	C. Ray Hartman	E. giganteum	H. arbutifolia	R. californica	P value
Parasitoids								
Ichneumonidae	4	38	8	6	0	5	12	0.0002*
Braconidae	8	53	11	5	5	5	8	0.0002*
Chalcidoidea	11	45	5	8	6	11	14	0.0002*
Cynipoidea	1	32	7	5	1	29	3	0.0024*
Tachinidae	1	1	1	2	5	3	1	0.5021
Generalist predators								
Coccinelidae	5	20	0	5	6	15	6	0.0156*
Syrphidae	3	3	0	6	10	1	0	0.0334*
Orius spp.	21	23	1	2	11	6	1	0.1016
Geocoris spp.	28	0	0	0	1	0	0	0.0002*
Nabis spp.	2	0	0	1	1	0	0	0.6441
Chrysopidae	0	13	3	9	1	10	13	0.1188
Hemerobiidae	1	6	2	5	0	3	13	0.0274*
Herbivore pests								
D. undecimpunctata undecimpunctata	3	52	0	2	2	10	1	0.0006*
A. trivittatum	0	27	0	2	1	4	2	0.0052*
P. pusilla	8	2	10	10	11	1	1	0.3853
L. hesperus	3	2	0	0	31	1	0	0.0002*
Aphididae	21	7	0	2	8	0	1	0.0550

Indicator values, ranging between 0 and 100, are the product of the relative abundance and frequency of the insect taxa collected at the hedgerow plant. An asterisk indicates a significant difference (P value < 0.05) among IVs for plant groups.

Differences in insect community composition among hedgerows corresponded to three major environmental gradients in both years. In 2005, NMS ordination axes 1, 2, and 3 captured 12.8, 14 0.3, and 16.1% of the variance in relative insect abundances, respectively (cumulative = 30.4%). Axis two corresponds to floral resource availability, while axes one and three indicate the influence of unmeasured environmental gradients (Fig. 4). In 2006 the three dimensions captured 11.7, 23.8, and 21.5% of the variance, respectively (cumulative 57%). Again, axis two corresponds to floral resource availability, while axis three corresponds to a temperature gradient where warmer sites are lower on the axis (Fig. 5). Axis one (not shown) indicates the influence of another environmental variable, which was not measured and was not apparent from different overlays.
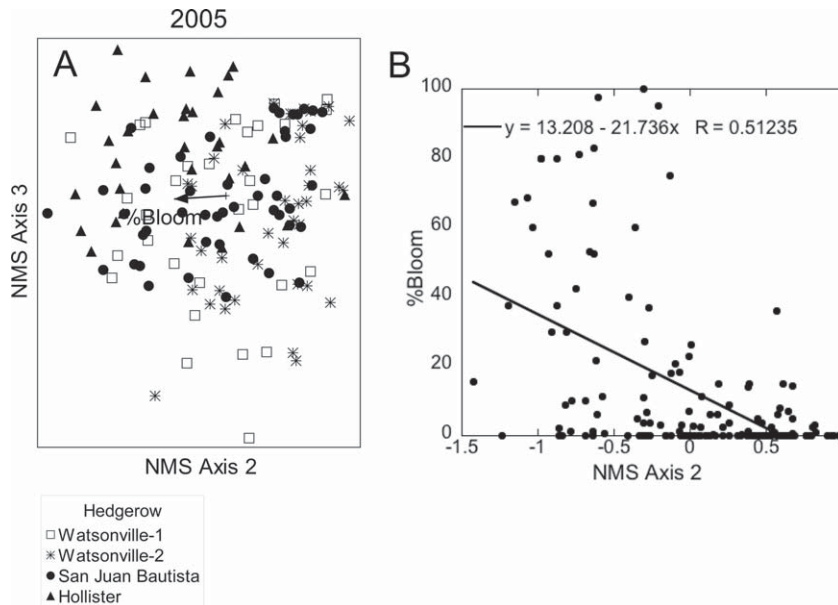

Fig. 4. Nonmetric multidimensional scaling ordination for the structure (abundance and frequency) of key taxa on hedgerow plants in 2005. Plots are coded by hedgerow sites. The two axes with the highest coefficient of variation (axis 2, $R^2 = 0.143$; axis 3, $R^2 = 0.161$) are shown. (A) Joint plot showing vectors of measured environmental gradients that correlate with the axes. (B) Correlation between % bloom and axis 2, $R^2 = 0.263$.
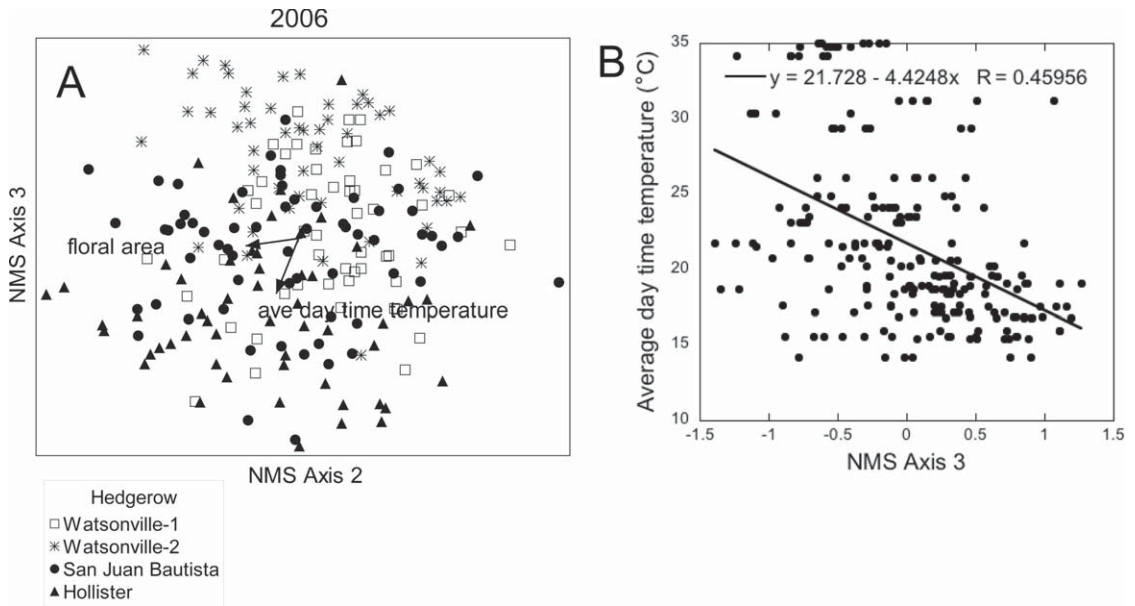
Fig. 5. Nonmetric multidimensional scaling ordination for the structure (abundance and frequency) of key taxa on hedgerow plants in 2006. Plots are coded by hedgerow sites. The two axes with the highest coefficient of variation (axis 2, $R^2 = 0.238$; axis 3, $R^2 = 0.215$) are shown. (A) Joint plot showing vectors of measured environmental gradients that correlate with the axes. (B) Correlation between average day time temperature and axis 3: $R^2 = 0.211$.

Association Between Floral Resource Availability and Insect Abundance. Each of the seven hedgerow plant species had a distinct flowering pattern, with only one or two plant species reaching peak bloom each month from April through October and bloom time lasting three to six consecutive months (Table 2). Despite the partitioned nature of floral resource availability among hedgerow plant species, the abundances of most natural enemies and pests on attractive plant species (as revealed by Indicator Species Analyses) was not explained by bloom intensity (R^2 values were <0.20). In 2005 the only significant positive association between insect abundance and floral resource availability of an associated plant species was between *Orius* spp. predators and *A. millefolium* ($R^2 = 0.52$). In 2006, *Orius* spp. abundance was positively associated with the floral area of *A. millefolium* ($R^2 = 0.21$), but the association was stronger with the amount of *B. pilularis* floral resources ($R^2 = 0.56$). Although *Orius* spp. abundance was associated with both female and male *B. pilularis* flowers, the correlation was slightly greater with male flowers ($R^2 = 0.60$) compared with female flowers ($R^2 = 0.49$). One caveat is that these regressions were done for only the inland sites where all coyote brush replicates bloomed (not all *B. pilularis* plant replicates bloomed by October at the coastal sites) and at one inland site all *B. pilularis* plants were female while at the other site they were all male. Notwithstanding our inability to control location as a contributing factor to *Orius* spp. abundance at flowering coyote brush, it appears that *Orius* most likely consumes *Baccharis* pollen and/or pollen feeding prey present on the flowers.

Despite the large and significant IVs for parasitic wasps on *B. pilularis* in comparison to other plant species, in both years of the study, floral resource availability of *B. pilularis* was not a significant predictor of parasitic wasp abundance (R^2 values were <0.10 for all analyses). However, when sites were analyzed separately we did find a significant positive relationship for Chalcidoidea at the inland site that had open female flowers of *B. pilularis* ($R^2 = 0.35$; $P < 0.0001$) and a slightly positive relationship for Cynipoidea at the inland site with flowering male (pollen) flowers ($R^2 = 0.26$; $P = 0.0003$) in 2006. In 2006 the association of *D. undecimpunctata undecimpunctata* and *A. trivittatum* with *B. pilularis* was partially explained by floral area; however, the R^2 values were low, 0.190 ($P < 0.0001$) and 0.231 ($P < 0.0001$), respectively.

Discussion

Perennial hedgerows established by coastal California vegetable growers tended to support a higher ratio of natural enemies to pests than did weedy borders, although there was high variation among hedgerows. In a similar California study of *in situ* hedgerows by Morandin et al. (2011), the proportion of beneficial insects captured was about twice as high on the perennial shrubs as on weedy areas adjacent to crop fields. Hedgerows may also support greater abundance of natural enemies than the more commonplace insectary plantings of annual exotic plants, because we captured more than four times the number of natural enemies on hedgerows than Hogg et al. (2011) captured with similar vacuum samples on insectary plant-

ings with *L. maritima, F. esculentum, Brassica* sp., *Phacelia tanacetifolia* Benth, *Borago officinalis* L. 'Alba' and several other annuals in Sonoma County, CA. Converting insect abundances found in other studies to ratios of natural enemies to pests for comparison (e.g., Hogg et al. 2011, Blaauw and Isaacs 2012), perennial insectary habitats outperformed annual plants. In addition, the average abundance of natural enemies vacuum sampled from a mix of mostly perennial species by Fiedler and Landis (2007) was about the same as found in our perennial hedgerows, though the two studies included different insect taxa. Thus, native perennials, though slower to establish, compare favorably and are more stable CBC habitat than either weedy field margins or flowering annual plants. Whether this potential is met depends in part, on creating an effective mix of plant resources to support the taxa needed for pest suppression on crops (Snyder et al. 2008).

Each hedgerow plant species, with the exception of *C. griseus*, hosted different relative densities of a generally overlapping insect community. Common yarrow was attractive to predatory and herbivorous homopterans. Perennial buckwheat was attractive to Syrphidae, an important natural enemy of aphids (van Emden 1965, Colley and Luna 2000, Bugg et al. 2008). Because syrphid flies tended to move away from hedgerow vegetation in response to the vacuum sampler, timed visual observations of Syrphidae visitation to hedgerow plants used in other studies may have provided a better measure of flower selectivity (Morandin et al. 2011 and Hogg et al. 2011). Perennial buckwheat was also attractive to lygus bugs in both years of the study. Morandin et al. (2011) also found this herbivore primarily on a perennial buckwheat species, *E. fasiculatum.* Coffeeberry was attractive to brown lacewings. Finally, coyote brush was an outstanding source of parasitic Hymenoptera, with Ichneumonidae, Braconidae, Chalcidoidea, and Cynipoidea all showing a high degree of faithfulness to *B. pilularis.*

The consistent attraction of *B. pilularis* to parasitic wasps across sampling periods and locations is congruent with Tilden's (1948) inventories of endemic arthropods on *B. pilularis* and Steffan's (1997) finding that Hymenoptera comprised ≈81% of all insect specimens from flowering *B. pilularis.* Attraction to resinous foliage (Girling et al. 2011), structural features, and endemic hosts for specialist and generalist parasitoids (Doutt 1961) may explain abundant parasitoids on both male and female plants, with or without flowers. Of the plant species tested, *B. pilularis* is the most common in the landscape. It is a dominant plant species in coastal and inland scrub habitat from the coastal-inland region of southern Oregon to Southern California (Doutt 1961). Thus, hedgerows that include coyote brush and connect to larger habitat fragments could potentially serve as dispersal corridors for parasitic wasps.

Coyote brush was also attractive to the spotted cucumber beetles in both years of the study. Our field observations and past studies (Tilden 1948, Steffan

1997) verify that *D. undecimpunctata undecimpunctata* use floral resources of *B. pilularis.* Morandin et al. (2011) also found that this ubiquitous pest was abundant on coyote brush in hedgerows of the Sacramento Valley, CA, along with natural enemies, when this shrub was blooming in fall. Pollen-feeding positively affects longevity, fecundity, and oviposition period of *Diabrotica* species (Naranjo and Sawyer 1987, Elliott et al. 1990); thus, careful monitoring of *B. pilularis* when in bloom is recommendable. If *D. undecimpunctata undecimpunctata* populations exceed acceptable levels in the hedgerow, it should be possible to reduce their number on hedgerows without negatively impacting the natural enemies by luring them into kairomone traps (Luna et al. 2006).

All of the six hedgerow plant species attracted herbivore pest species to a certain extent. *E. giganteum* had the lowest natural enemy to pest ratio in 2006 and was associated with *L. hesperus.* Thus, perennial buckwheat may not be a suitable choice in vegetable systems that have strawberries in the rotation. In contrast, *B. pilularis* and *A. millefolium,* which had high natural enemy to pest ratios, but hosted dissimilar insect communities, would be particularly suitable plant species for hedgerows designed for CBC. Screening a larger number of native perennial plant species that are selective to natural enemies and not pest species would provide farmers and landscape managers with information to fine tune hedgerow design for optimal CBC habitat (Baggen et al. 1999, Begum et al. 2006).

Contrary to our prediction, floral resource availability was not a strong predictor of key insect abundance on preferred hedgerow plant species, except for *Orius* spp. Although we observed several taxa, including Sryphidae, Hymenoptera, Chrysopidae, Chrysomelidae, and Coccinellidae, foraging on the nectar or pollen in flowers, many of these insects were abundant on hedgerow plants when they were not flowering. Observations of insect activity made before vacuum sampling showed that insect natural enemies use hedgerow plants to rest, mate, pupate, take shelter from windy conditions and high temperatures, and to forage for prey. Although refuge and alternate prey are often mentioned as important to CBC habitat (Wratten et al. 1998, Landis et al. 2000), researchers routinely sample insectary plant species only when in bloom, and focus primarily on floral resources, which do not fully explain natural enemy attraction (e.g., Fiedler and Landis 2007, Forehand et al. 2006, Witting et al. 2007).

NMS provided a useful nonparametric tool for visualizing the similarities in insect community structure between hedgerow sites. Clustering of plots by location was more evident in the ordination for 2006 and MRPP results confirm that location was a significant factor on insect community structure. Floral resource availability explained some of the variation in community composition at hedgerow plots in both years; however, the 2006 NMS ordination revealed an additional temperature gradient that corresponded to hedgerow location. MRPP pair-wise comparisons showed that cooler, coastal sites were most similar in

insect community composition, while the coolest site and warmest site were most dissimilar. Generally, natural enemy abundances were higher in warmer sites, but certain groups, namely Ichneumonidae, were more abundant at cooler sites. NMS identified one to two other unmeasured environmental gradients that influenced relative abundance and frequency of natural enemy and pest populations on hedgerow plants. Factors such as natural enemy host range (Doutt 1961), crop diversity (Brown 2012), cropping and management practices (Nentwig 1988, Thorbek and Bilde 2004), density of primary and alternative host or prey populations (Starý and González 1991), or the proportion and composition of noncrop habitat in the landscape (Roschewitz et al. 2005, Bianchi et al. 2006, Werling et al. 2011) may influence variation in insect community structure among hedgerow plants and locations. For example, the extremely high abundances of *D. undecimpunctata undecimpunctata* in the Hollister hedgerow, according to the farmer, reflected long-term, local population patterns of that pest because of the production of melon and high emigration of beetles to the field margins later in the season in response to melon harvest.

Although habitat management for CBC requires a favorable assortment of resources to enhance and maintain natural enemies near crop fields (Pickett and Bugg 1998) and habitat that supports a high ratio of natural enemies to pests increases the potential for biological control, increased pest mortality on crops requires that those natural enemies move sufficiently between noncrop habitat and crops. Our mark-recapture studies on these hedgerows and other studies on predators (e.g., Syrphidae, Coccinellidae) and parasitoids (e.g., Ichneumonidae) demonstrate movement between crop fields and field margins (Wratten and Thomas 1990, Long et al. 1998, Schellhorn et al. 2004, T.L.P.G., unpublished data). However, sticky trap captures within hedgerow fields did not reflect a greater ratio of natural enemies to pests in comparison to fields with weedy margins. The lack of a significant increase in natural enemies within the field raises questions about the magnitude of the effect of these hedgerows on biological control of crop pests, at least later in the season (August and September). Increasing natural enemy diversity has been shown to have variable (positive, negative, and neutral) effects on prey and host suppression (Straub et al. 2008). An increase in intraguild predators within hedgerows could reduce natural enemy populations, potentially resulting in decreased pest mortality (Rosenheim 2005, Prasad and Snyder 2004). However, greater habitat complexity and increased food supplementation (pollen and nectar) has also been shown to weaken intraguild predation (Shakya et al. 2009).

Testing the efficacy of native perennial plants as CBC habitat using an on-farm research design limited our choice of plants and ability to control environmental variables, but with the aid of nonparametric procedures increased realism with respect to how hedgerow plants perform in concert and how insect associations with them vary with locality. We propose that perennial hedgerows can be designed through plant species selection to support particular beneficial insect taxa, but plant resources beyond floral availability may be critical in providing structural refuge, alternative prey, and other attractive qualities for some key groups of natural enemies. Like the wild blackberries in the classic Doutt and Nakata (1965) study, hedgerows may support natural enemies earlier in the season and over longer periods of time than annual blooming plants. However, further research is needed to rigorously assess the effectiveness of hedgerows at providing biological control of key pests within adjacent crop fields, or whether a combination of infield annual insectaries and hedgerows provides any synergistic benefit.

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