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Influence of the surrounding landscape on crop colonization by a polyphagous insect pest

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Abstract

Landscape composition plays an important, but poorly understood, role in the population dynamics of agricultural pest species with broad host ranges including both crops and weeds. One such pest, the generalist plant bug *Lygus hesperus* Knight (Hemiptera: Miridae), is a key cotton pest that feeds on various hosts differing in quality in California's San Joaquin Valley (USA). We investigated the effects of 15 common crops and uncultivated agricultural land on *L. hesperus* populations, by correlating the densities of *L. hesperus* in focal cotton fields with the areas of the 16 crops in surrounding rings. Insect counts were provided by private pest-control advisors, and spatial data were obtained from Kern County records. We first calculated Spearman's partial correlation coefficients on an annual basis for each crop separately, and then performed a meta-analysis of these correlations across years to describe the overall effect of a particular crop on *L. hesperus* after the effects of the 15 other crops are removed. Consistent with studies conducted in other areas, *L. hesperus* density was positively correlated with safflower, and negatively with cotton. *Lygus hesperus* density was also correlated with several other crops that are often not considered in pest management, including grape, oat, and onion (positive correlations), and almond, pistachio, and potato (negative correlations). *Lygus hesperus* density was also found to be negatively correlated with alfalfa and positively correlated with uncultivated habitats, a relationship that receives mixed support in the literature. Several other crops tested were not significantly correlated with *L. hesperus* densities in focal cotton fields, suggesting a neutral role for them in *L. hesperus* dynamics. The improved understanding of the effects of a greater variety of crops on *L. hesperus* population dynamics will be useful in the design of agricultural landscapes for enhanced management of this important polyphagous pest.

Introduction

Arthropod pests in annual agroecosystems are often polyphagous, display distinct preferences for particular hosts, and demonstrate high mobility (Kennedy & Storer, 2000). Their life cycles usually depend on the exploitation of a series of crop and weed hosts. These hosts can affect the population dynamics and spatial distributions of generalists in a variety of ways. For example, on high-quality hosts the birth rate may be much greater than the death rate, so populations may grow rapidly. In temporally unstable ecosystems like agroecosystems, disturbances such as harvest or senescence of a high-quality host could force pest populations to emigrate; thus, high-quality hosts might act as a source of individuals for surrounding fields. Alternatively, these high-quality hosts might act as trap-crops, attracting pests away from neighboring crops throughout the growing season if the high-quality hosts remain attractive (often through careful management by the grower). Low-quality host plants might have the opposite effect on insect herbivore population dynamics, depressing pest densities. Hosts could have no observable effect on the growth rate of insect populations in target crops and could instead affect the spatial distribution of

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generalists by reducing the apparency of other hosts (Vandermeer, 1989). Other crops in the landscape that are not hosts for generalists might act as conduits for insect movement, through which individuals move quickly to reach suitable hosts. Thus, knowledge of host and non-host associations is important for the management of the landscape configuration to modify pest density.

The relative importance of particular habitat patches on pest population dynamics has been investigated in focal-patch landscape studies (Brennan et al., 2002), where correlative methods have been used to quantify the influence of particular patches on the relative abundance of a focal species (Pope et al., 2000; Carrière et al., 2004, 2006, 2012; Ricci et al., 2009; Bahlai et al., 2010; Logan et al., 2011). The data sets used in these studies, however, are often modest in size, due to the high sampling effort required to estimate the density of a focal species in a large number of fields and to characterize the landscape composition. Although relatively small data sets can provide crucial tests of the role of particular habitat types for herbivores (e.g., patches of common buckthorn, *Rhamnus cathartica* L., as a source of soybean aphid, *Aphis glycines* Matsumura; Bahlai et al., 2010), small data sets may impose severe limits on the power of statistical tests and the ability to assess the effects of a large number of potentially important habitats on pest dynamics.

One practical approach in generating larger data sets for landscape ecological investigations of agricultural pests is to use pre-existing survey data. This is one type of contributory citizen science project (sensu Bonney et al., 2009), where professional researchers analyze citizens' recorded observations to inform a study designed by professional researchers (Bonney et al., 2009; Miller-Rushing et al., 2012). Typically, survey/citizen science data sets are substantially larger than those collected by researchers, which could give studies using survey data a greater power of resolution (Rosenheim et al., 2011). Caution is required when working with such data sets, however, because the data have the potential to be collected in different ways, measure different variables, or contain errors (Rosenheim et al., 2011; Miller-Rushing et al., 2012; Bates et al., 2013). One source of pre-existing data is the insect scouting data generated by private pest management consultants, who monitor insect pest densities in commercial agricultural fields. Although private consultants are usually not professional scientists, they often have more experience in sampling economically relevant arthropods than even the most practiced researcher. This experience, coupled with the fact that the consultants' livelihoods depend on producing useful estimates of pest densities, give us confidence in the quality of these pre-existing survey data. In our study, we used such data sets to substantially expand the set of habitats to be evaluated as potentially important drivers of the colonization of cotton, *Gossypium hirsutum* L. (Malvaceae), by the important pest, *Lygus hesperus* Knight (Hemiptera: Miridae).

Lygus hesperus is a polyphagous insect pest for which the importance of management at the landscape scale has been recognized since the 1960s (Stern et al., 1964). In California's San Joaquin Valley, *L. hesperus* is known to feed on over 100 species of plants in 24 families (Scott, 1977). *Lygus hesperus* is highly mobile (Sivakoff et al., 2012), and in the course of the year populations complete several generations, often while exploiting a sequence of crop and weed hosts. *Lygus hesperus* can cause serious economic losses in cotton, and was found to move into cotton from other preferred hosts when these were becoming unsuitable (Goodell, 2009). Its hosts include alfalfa (*Medicago sativa* L.), a perennial crop that becomes suitable before cotton and is harvested monthly for hay (Stern et al., 1964); safflower (*Carthamus tinctorius* L.), a potential biofuel and an annual crop that begins to senesce while cotton is vulnerable to *L. hesperus* feeding (Mueller & Stern, 1974); and a diversity of weeds that often grow in fallow fields, reach maturity, and begin to dry out once winter or spring rains cease (Fleischer & Gaylor, 1987; Barlow et al., 1999).

Carrière et al. (2006, 2012) used various correlation and regression analyses to examine the relationships between areas of crops that have long been considered sources, or sinks, for *L. hesperus* and the observed *L. hesperus* population densities in focal cotton fields. Using rank-based statistics, they found either positive, negative, or no relationship between the *L. hesperus* density observed in cotton and the presence of a limited number of habitats in the neighborhood; less than seven habitats were considered. Their correlation and regression analyses revealed consistent source or sink effects of some habitats and variable effects of some others, over seasons or years. The authors used their findings to suggest specific landscape configurations to reduce *L. hesperus* damage to cotton (Carrière et al., 2006, 2012).

Although several key crops (e.g., alfalfa, cotton, safflower, and uncultivated agricultural land) have been shown to influence *L. hesperus* populations, the effects of other crops have not yet been explored. *Lygus hesperus* uses many other host plants commonly found in agricultural settings in California (Table 1), and the presence of multiple potential hosts complicates the management of this pest in susceptible crops such as cotton (Barlow et al., 1999). The work presented here builds on the successes of earlier studies (Carrière et al., 2006, 2012), and extends the analytical approach to strictly pre-existing data sets

Table 1 List of 16 crops and the status of each crop as a host plant for *Lygus hesperus*. Here, we define a host as a plant on which *L. hesperus* has been documented to feed. Also listed is the expected effect of the presence of each crop on *L. hesperus* density in adjacent cotton fields based on previous studies. A '+/−' expected relationship indicates a habitat reported with both positive and negative associations in the literature, and a '0' indicates no a priori expectation of a relationship

Crop	Scientific name	Feeding by *L. hesperus* documented?	Expected relationship to *Lygus hesperus* density	References
Alfalfa	*Medicago sativa* L.	Yes (Scott, 1977)	+/−	Stern et al. (1964); Carrière et al. (2006, 2012)
Almond	*Prunus dulcis* (Mill.) D.A. Webb	Unknown	0	
Carrot	*Daucus carota* L.	Yes (Scott, 1977)	0	
Cherry	*Prunus avium* (L.) L.	Unknown[1]	0	
Maize	*Zea mays* L.	Yes (Scott, 1977)	0	
Cotton	*Gossypium hirsutum* L.	Yes (Scott, 1977)	−	Carrière et al. (2006, 2012)
Grape	*Vitis vinifera* L.	Unknown[2]	0	
Oat	*Avena sativa* L.	Yes[3] (Barlow et al., 1999)	0	
Onion	*Allium cepa* L.	Yes (Fye, 1984)	0	
Pistachio	*Pistacia vera* L.	Yes (Rice et al., 1985)	0	
Potato	*Solanum tuberosum* L.	Yes (Scott, 1977)	0	
Safflower	*Carthamus tinctorius* L.	Yes (Scott, 1977)	+[4]	Mueller & Stern (1974); Carrière et al. (2012)
Sugar beet	*Beta vulgaris* L.	Yes (Scott, 1977)	+	Carrière et al. (2012)
Tomato	*Solanum lycopersicum* L.	Yes[5](Scott, 1977)	−	Carrière et al. (2012)
Uncultivated	Variety of weedy host species[6]	Yes (Barlow et al., 1999)	+/−	Carrière et al. (2006, 2012)
Wheat	*Triticum* spp.	Unknown[7]	0	

[1] Feeding documented for *Lygus lineolaris* (Palisot de Beauvois) (Hutson, 1953).
[2] Feeding documented for *L. lineolaris* (Bruner, 1895).
[3] Feeding documented on wild oat (*Avena fatua*).
[4] Carrière et al. (2012) found that effects of safflower were positive in 2 years of their study (2007 and 2008), but negative in 2009.
[5] Listed under the synonym *Lycopersicon esculentum* Mill.
[6] For a list of potential species, see Barlow et al., 1999.
[7] Feeding documented for *Lygus rugulipennis* Poppius (Varis, 1991).

generated by private pest control advisors, who actively monitor insect pest densities in commercial agricultural fields. The use of such data allowed us to investigate an expanded list of candidate crops and non-crop weeds that might affect the density of *L. hesperus* in focal cotton fields. To determine the overall effect (i.e., positive, negative, or neutral) of a particular host, we performed meta-analysis on 6 years of data. Earlier study examining the influence of other crops on *L. hesperus* density in cotton (Stern et al., 1964; Mueller & Stern, 1974; Carrière et al., 2006, 2012) provided us with expected roles for several crops, but not for all (Table 1).

Materials and methods

Survey data

We used survey data collected by private pest management consultants to produce large data sets of *L. hesperus* densities in commercial cotton fields grown in Kern County, California, between 2003 and 2008. Each cotton field included in the data set had a variety of information associated with it, including *L. hesperus* density, pesticide use, and spatial context.

Lygus hesperus density was estimated approximately weekly during the period of crop sensitivity to *L. hesperus* damage (typically late May through early August). These data are reported as sweep net samples, taken at several locations in a field and then averaged to obtain an average density estimate for that field in that week. Data were available for 102 fields in 2003, 134 fields in 2004, 130 fields in 2005, 90 fields in 2006, 88 fields in 2007, and 55 fields in 2008, for a total of 599 records. Of these fields, 74% (443/599) were sampled in more than 1 year.

Pesticide use data were provided by the pest control advisors and supplemented with data from the California Department of Pesticide Regulation's web-based Pesticide Use Reporting System (Department of Pesticide Regulations, 2000). California farmers must, by law, report all applications of agricultural chemicals (Bronzan & Jones, 1989).

Spatial context is available as a digital map of geographic information system (GIS) shapefiles showing agricultural fields and prepared by the Kern County Department of Agriculture and Measurement Standards (http://www.co.kern.ca.us/gis/downloads.asp). The information associated with these spatial data included the area and land use of each field. Agricultural fields were originally digitized to provide shapefiles by GIS analysts for Kern County, based on growers' maps in 2000, and these shapefiles were updated and validated each year with input from individual growers (M Sabin, pers. comm.). GIS maps were obtained for 2003–2008, and were validated with grower-provided paper ranch maps.

Response variable: mean *Lygus hesperus* density

Lygus hesperus density estimates were calculated from samples collected weekly in the early phase of the cotton growing season (typically from the end of May to the end of June) and prior to any pesticide application targeting *L. hesperus*. This subset of samples was chosen because the initial colonization process, when cotton is vulnerable to *L. hesperus* feeding, was of interest and because treatment effects might be confounded with landscape effects on pest population dynamics (Ricci et al., 2009). The mean density of *L. hesperus* (adults and nymphs combined) was calculated from the day of the first recorded sample until 30 June or until the first pesticide application targeting *L. hesperus* was made if this occurred prior to 30 June. Because that time interval was not the same for all the cotton fields, the mean density of *L. hesperus* was calculated as a weighted regression: the density of *L. hesperus* on the Y-axis was plotted against the sampled day on the X-axis, and the mean *L. hesperus* density was estimated as the area under the resulting curve, divided by the number of days covered by the sampling period. This estimation method allows for comparability across cotton fields. Modifications like this are especially important with survey/citizen science data sets that often vary in sampling frequency (Bates et al., 2013). This calculation was done using COTTONFORMATICS, a relational database software application developed for this project (Ten2Eleven Business Solutions, Davis, CA, USA).

Explanatory variables: Landscape variables

The study area is an agricultural landscape of ca. 1 250 km^2 at the southern end of the San Joaquin Valley, in western Kern County (WGS84 system coordinates: from 35°7′30″ to 35°25′32.6″N, and from 119°30′50.4″ to 118°53′24″W). Using ArcGIS (ESRI, 2011), we identified the 15 most common crops located within 3 km of our focal cotton fields in each digital crop map (one crop map per year, 2003–2008). To this list, we added safflower, a crop that was rare in these landscapes but known to be an important host for *L. hesperus* (Mueller & Stern, 1974). This resulted in a master list of 16 crops (with uncultivated agricultural land included as a crop type) characterizing 76–81% of the area of the 3 km rings surrounding focal cotton fields (Table 1).

Following the approach used by Carrière et al. (2004, 2006, 2012), we used ArcMap 10 (ESRI, 2011) to draw three concentric rings around the edge of each focal cotton field at distances of 1 000, 2 000, and 3 000 m from the edge of the focal field. We chose the scale of 1 000 m from earlier work in which the mean distance flown by *L. hesperus* moving from a harvested alfalfa field into surrounding cotton was estimated to be 1 157 ± 114 m (Sivakoff et al., 2012). We then measured the area of each of the 16 crops (m^2) within each ring using ArcMap (Figure 1).

Statistical analysis

To test the 'pure' effect of a particular crop on *L. hesperus* density, we correlated the area of each crop in each ring to *L. hesperus* density in the focal cotton field after partialling out the effects of the 15 other crops. The resulting partial correlation coefficients were adjusted for spatial autocorrelation among focal cotton fields. More specifically, the areas of each crop were rank-transformed and Spearman's rank-based partial correlations were used to measure the effect of the area of crop i ($i = 1–16$) in ring j ($j = 1–3$) on *L. hesperus* density, given the areas of crops other than i in ring j. We chose to use non-parametric (rank-based) statistics because the assumption of normality was not met in the untransformed data, precluding the use of parametric correlative methods. The number of our explanatory variables was large, resulting in increased likelihood of having influential outliers in analyses, and rank transformation reduces the risk that outliers have disproportionate influences on the results.

We accounted for spatial autocorrelation among focal cotton fields by adjusting the number of degrees of freedom in the t-tests used to assess the significance of partial correlations. This was accomplished through the calculation of an effective sample size, defined as 1 + the inverse of the variance of the sample correlation coefficient (Dutilleul, 1993; Alpargu & Dutilleul, 2006). Customized programs were written in MATLAB version R2008a (MathWorks, Natick, MA, USA) to perform these statistical analyses. A significant positive partial correlation coefficient r_{ij} means that the presence of habitat i in ring j is positively associated with *L. hesperus* density in focal cotton fields after the effects of other habitats in the same ring are taken into account; a significant negative partial correlation coefficient suggests a negative association; and a

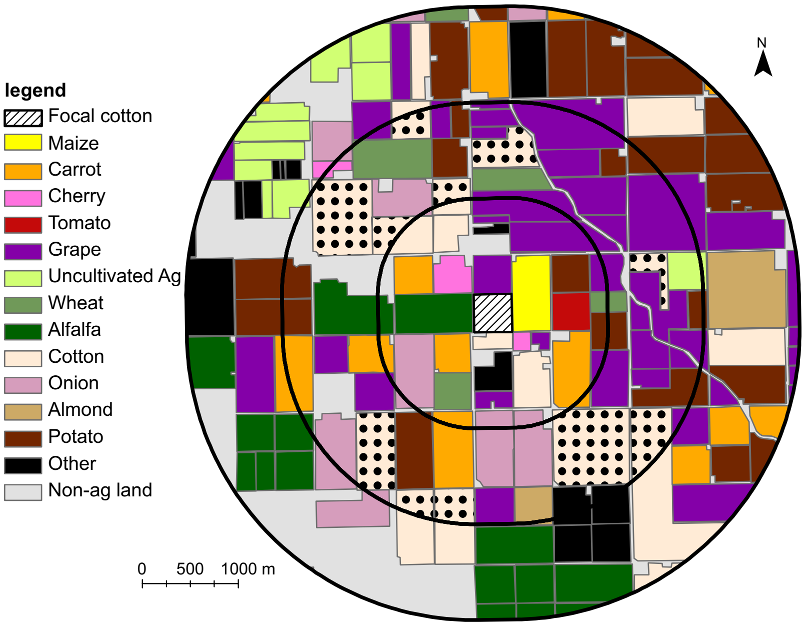

Figure 1 A focal cotton field (slashed black lines) surrounded by three concentric rings. The width of each ring is 1000 m. The cotton area associated with the 2000 m ring is highlighted with black dots.

non-significant partial correlation coefficient means the null hypothesis that habitat i in ring j has no effect on *L. hesperus* density in focal cotton fields cannot be rejected.

We explored the possibility of pooling the data across the 6 years (2003–2008) to perform a global analysis, but the results of a coregionalization analysis with a drift (CRAD; Pelletier et al., 2009a,b) suggested that this would not be appropriate; for details, see Appendix A. We therefore adopted an alternative approach based on a synthesis of our results across the multi-year data set, by performing a meta-analysis of the partial correlation values obtained in the six annual analyses; thus, the overall effect of each of the 16 crops on mean *L. hesperus* density was described. For each habitat in each ring (e.g., alfalfa in the 2 000 m ring), we estimated a common metric of effect size across the 6 years, here the common partial correlation coefficient (Hedges & Olkin, 1985; Gurevitch & Hedges, 2001), which resulted in a total of 48 (16 habitats × 3 rings) common partial correlation coefficients. First, each r_{ijk}, where $i = 1–16$ crops, $j = 1–3$ rings, and $k = 1–6$ years, was z-transformed to normalize the distribution of r and make the variance independent of the population correlation (Hedges & Olkin, 1985). For given i and j, a common coefficient z_{ij+} was then calculated using a fixed-effect model for meta-analysis, which consisted of a linear combination of z_{ijk} $(k = 1, \ldots, 6)$ weighted by the corresponding sample size; fixed-effect models assume that the studies being compared share a common true effect size and that differences between studies are the result of sampling error (Gurevitch & Hedges, 2001). Then, z_{ij+} was back-transformed, as were the lower and upper bounds of its confidence interval at 95% level. A habitat exhibited a statistically significant effect on mean *L. hesperus* density if the resulting confidence interval was not including zero.

Results

Our meta-analysis identified significant effects for 10 of 16 (63%) crops on mean *L. hesperus* density in focal cotton fields across the 6 years of data (Figure 2). Seven of the 48 (15%) crop × ring combinations examined were positively and significantly associated with *L. hesperus* density; the five crops involved are safflower, oat, grape, onion, and uncultivated agricultural land. Eight of the 48 crop × ring combinations examined were negatively and significantly associated with *L. hesperus* density in focal cotton fields; the five crops involved were almond, pistachio, alfalfa, potato, and cotton. Six crops (carrot, maize, tomato, sugar beet, wheat, and cherry) had no significant effect on *L. hesperus* density, suggesting that the presence of these habitats in the agricultural landscape has a neutral effect on *L. hesperus* population dynamics in cotton.

The spatial scale (ring width) at which associations were found to be significant was not consistent across crops.

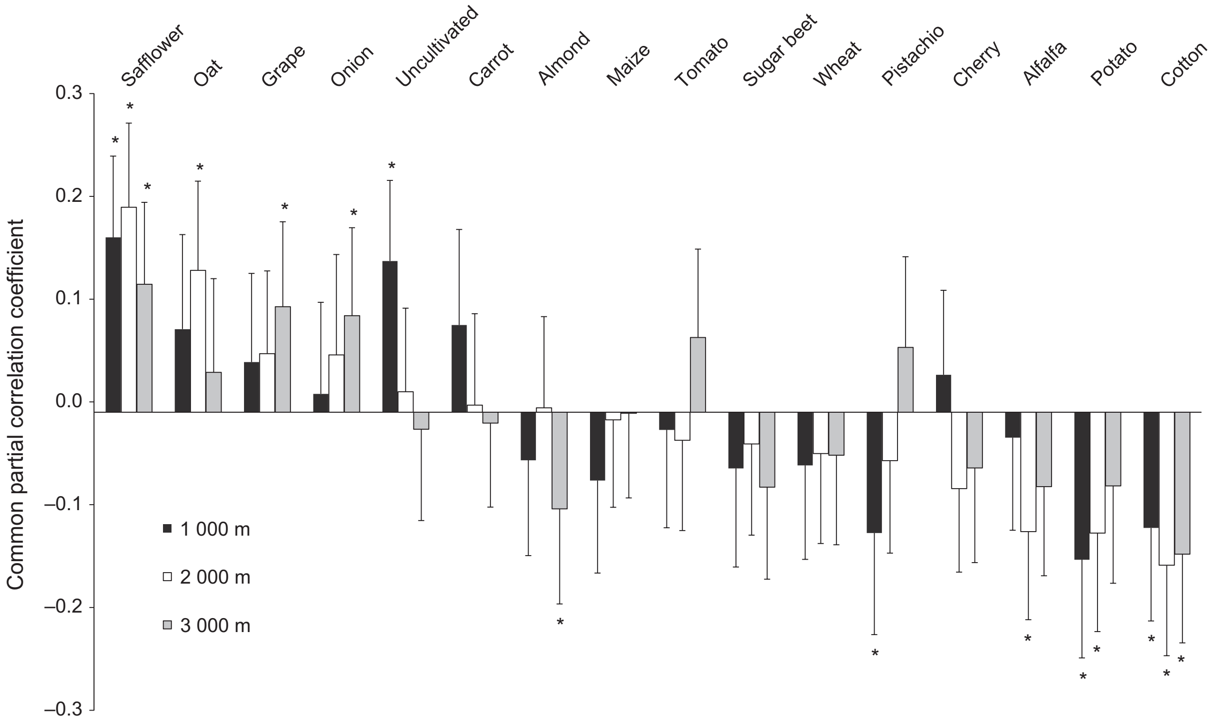

Figure 2 Mean (+ 95% confidence interval) partial correlation coefficients for all crops and across the three concentric rings. Asterisks (*) indicate a partial correlation coefficient that is significantly different from zero. If a partial correlation coefficient is positive and significant for a ring, it indicates that presence of the crop within that ring is associated with increased *Lygus hesperus* density in focal cotton fields after removal of the effects of other habitats in the same ring and any interior rings. If the partial correlation coefficient is negative and significant for a ring, the effect of that crop, when present in that ring, is a decreased density of *L. hesperus* in focal cotton fields. Partial correlation coefficients were calculated across the 6 years of data in a meta-analysis.

Only safflower and cotton demonstrated significant (P<0.05) correlations at all three spatial scales. With the exception of potato, significantly correlated with *L. hesperus* density at both the 1 000 and 2 000 m rings, significant associations for all other crops occurred at a single ring distance (Figure 2). Uncultivated agricultural land and pistachio were significantly correlated with *L. hesperus* density at the 1 000 m ring, alfalfa and oat at the 2 000 m ring, and grape, onion, and almond at the 3 000 m ring.

Discussion

Overall effects of crops

Using a large survey data set, we found that out of the 16 crops examined (through 48 crop × ring combinations), five habitats had positive correlations with *L. hesperus* density, five others had negative correlations with *L. hesperus* density, and six did not have a significant effect on *L. hesperus* density. The scale(s) of the effects varied with the crop.

Our finding that several crops are positively associated with *L. hesperus* density is generally in agreement with previous studies (Stern et al., 1964; Mueller & Stern, 1974; Sevacherian & Stern, 1975; Barlow et al., 1999; Goodell et al., 2002; Carrière et al., 2006, 2012; Goodell & Ribeiro, 2006; Goodell, 2009). Safflower, a crop generally considered to be an important source of *L. hesperus*, was positively correlated with *L. hesperus* density at all three ring distances despite being uncommon in the landscape (<1% of the area of the 3 000-m rings surrounding focal cotton fields). The integrated pest management (IPM) community has long recognized this relationship; since the 1970s, farmers have applied insecticides to mature safflower to preempt *L. hesperus* movement to nearby cotton fields (Mueller & Stern, 1974; Goodell, 2009). In a study conducted in the Fresno and Kings counties of the San Joaquin Valley, Carrière et al. (2012) found a significant positive association between safflower abundance and *L. hesperus* density in cotton in 2 years, but a significant negative association in a 3rd year. This change corresponded with higher application rates of insecticides to safflower for *L. hesperus* control in the 3rd year, supporting the idea that inter-annual changes in safflower management can significantly affect *Lygus* outbreaks in cotton

(Mueller & Stern, 1974; Goodell, 2009). In addition, we found a significant positive association with uncultivated agricultural land, the scale of this effect extending to 1 000 m. This land is usually fallow (M Sabin, pers. comm.) and likely contains a collection of non-crop weed hosts. A variety of weeds are known to be hosts of *L. hesperus*, including *Hemizonia kelloggii* Greene (tarweed; Goodell & Ribeiro, 2006), *Salsola kali* L. var. *tenuifolia* Tausch (Russian thistle; Goeden & Ricker, 1968), *Capsella bursa-pastoris* (L.) Medik. (shepherd's purse), *Stellaria media* (L.) Vill. (common chickweed), *Senecio vulgaris* L. (common groundsel), *Poa annua* L. (annual bluegrass), and *Avena fatua* L. (wild oat; Barlow et al., 1999). Carrière et al. (2006) also found weeds to be an important source of *L. hesperus* in Arizona (USA), with the positive effect extending to 500 m from focal cotton fields. The scale of the effect of uncultivated agricultural land in our study is consistent with that in Carrière et al. (2006). However, in the Fresno and Kings counties of the San Joaquin Valley, Carrière et al. (2012) found consistent negative associations between *L. hesperus* density in focal cotton fields and areas of uncultivated habitats between June and August. Considering these results together suggest that the effect of a particular crop or habitat on *L. hesperus* density in cotton may vary across landscapes. Further investigation is needed, as this variable effect of uncultivated vegetation may be a result of several factors, including differences in the period investigated, management practices, and weed and crop composition.

Several other crops that had not previously been considered in *L. hesperus* management were found to be positively associated with *L. hesperus* density. One such crop is grape, which in our analysis is a combination of table, wine, and raisin grapes. *Lygus lineolaris* (Palisot de Beauvois), a closely related species of *L. hesperus*, has been observed to feed on grape (Bruner, 1895, cited in Wheeler, 2001). More likely, however, vineyards may act as a source of *L. hesperus* because they have cover crops or contain non-crop weed hosts at their margins (Ohlendorf et al., 1996), and it is these plants that are hosts of *L. hesperus*. We also found that onion was positively correlated with *L. hesperus* density, which is in agreement with results presented by Goodell & Ribeiro (2006).

Alfalfa has long been considered a key host for *L. hesperus*, recognized as an important source of *L. hesperus* when it is harvested (Stern et al., 1964; Sevacherian & Stern, 1975), but also thought to act as a trap-crop for *L. hesperus* when managed with strip-cutting (Stern et al., 1964, 1969; Summers et al., 2004). According to a 2000 survey, strip-cutting of alfalfa has been adopted by 51% of California cotton growers (Brodt et al., 2007; Goodell, 2009). Goodell & Lynn-Patterson (2005) observed a negative relationship between the area of alfalfa in the agricultural landscape and the number of pesticide applications targeting *L. hesperus* in cotton. This observation suggests that when alfalfa is properly managed, it can attract *L. hesperus* away from nearby cotton. This idea has support in the literature (Stern et al., 1969; Rakickas & Watson, 1974; Stewart & Layton, 2000), and was supported in our study by the negative correlation between alfalfa and *L. hesperus* density. Carrière et al. (2012) found both positive and negative associations between area of forage alfalfa and *L. hesperus* density in cotton, and suggested that such variation may be because of temporal or regional variation in the management of this crop. Goodell (2009) suggested a potential mechanism for the negative correlation that we observed, namely that a landscape with many alfalfa fields provides preferred habitats for *L. hesperus* displaced by the harvest of nearby alfalfa fields. The option to move into a preferred host like alfalfa would reduce the likelihood of *L. hesperus* moving into cotton. This scenario relies upon an asynchronous harvest of alfalfa fields in an area, which is almost always the case because of the limited harvesting resources of individual growers and the scale of the 'zone of influence' (sensu Carrière et al., 2004) of alfalfa. We suggest that an appropriate zone of influence for alfalfa is 2 000 m, the distance at the limit of the second ring in our study, where alfalfa was significantly negatively correlated with *L. hesperus* density.

Several other crops emerged from our analyses as negative correlates of *L. hesperus* density, including almond, pistachio, and cotton. Goodell & Ribeiro (2006) identified non-bearing almonds as a source of *L. hesperus*. This discrepancy is likely a result of differences in orchard weed management. Non-bearing orchards usually support large populations of weeds, many of which being high-quality hosts of *L. hesperus*. Although there is some variability in the management of the floors of bearing orchards, active almond and pistachio orchards are generally almost free of weedy vegetation (PB Goodell, pers. comm.), and almond trees themselves are not known to be hosts of *L. hesperus*. *Lygus hesperus* is known to feed on pistachio (Rice et al., 1985; cited in Wheeler, 2001), but this is not considered a preferred host (Goodell et al., 2002). As reported by Carrière et al. (2006, 2012) and confirmed here, the presence of cotton in the neighborhood is significantly negatively associated with *L. hesperus* density in focal cotton fields.

Two crops not generally considered important in the management of *L. hesperus*, oat and potato, emerged as having strong effects on pest densities in focal cotton fields. Both crops are considered hosts for *L. hesperus*, but the host status of oat, *Avena sativa* L., has been confirmed only for *Lygus rugulipennis* Poppius and for *L. hesperus* in wild oat, *A. fatua* (Varis, 1991; Barlow et al., 1999). Even though the importance of potato has not been acknowledged in the literature, growers appear to be aware of its importance. One reason why the pest management community has yet to acknowledge the influence of potato may be that the harvest of this host is staggered over the cotton growing season, and some growers who produce both cotton and potato pre-emptively spray potato fields prior to harvest to prevent *L. hesperus* movement (JA Rosenheim, unpubl.). Further investigation is needed to clarify this interaction. This is also true for the positive relationship with oat, which likely is a host of *L. hesperus* (Barlow et al., 1999), but whose feeding does not generate economic damage. As a result, the presence of *L. hesperus* may be largely ignored or invisible to the grower. Within our study area, oat is grown as a rain-fed, low-input crop with limited weed control, suggesting that the presence of weedy hosts may explain the observed relationship between *L. hesperus* density and oat.

Design of agricultural landscapes

An understanding of the relationships between *L. hesperus* density and the presence of particular crops in the agricultural landscape, in addition to the scale of these relationships, could allow farmers to manage *L. hesperus* over the landscape in a way that minimizes *L. hesperus* pressure on vulnerable crops like cotton. Several general recommendations emerge from our results. First, growers should avoid planting vulnerable crops in proximity to crops positively associated with pest density. In the *L. hesperus* system, this means not planting cotton within a 3 000 m distance from safflower, as our study indicates that the influence of safflower on *L. hesperus* density in cotton fields extended at distances up to 3 000 m. A second recommendation would be to manage nearby crops for weedy hosts of *L. hesperus*. A third recommendation would be to plant vulnerable crops near crops that are negatively correlated with pest density, thus effectively using negatively associated habitats as traps for pests. This technique has been implemented to a limited extent in the San Joaquin Valley, with the general result that the presence of properly managed (i.e., strip-cut) alfalfa reduces *L. hesperus* density in cotton (Stern et al., 1969; Goodell, 2009). Our results indicate that alfalfa fields could contribute in reducing *L. hesperus* density in cotton fields located at distances of up to 2 000 m.

Another landscape design recommendation that may reduce the impact of pests on vulnerable crops, if these are themselves negatively correlated with pest density, is to cluster the vulnerable crops instead of spreading them evenly over the agricultural landscape. This has been proposed for cotton to reduce *L. hesperus* pressure (Carrière et al., 2006, 2012) and for potato to protect against the Andean potato weevil (*Premnotrypes* spp.; Parsa et al., 2011). It has also been demonstrated theoretically that aggregating multiple fields of the same vulnerable crop can reduce pest densities (Segoli & Rosenheim, 2012).

Pre-existing survey data sets offer novel opportunities for IPM researchers. One advantage of using pre-existing survey data sets is that they are generally substantially larger than those collected by researchers, providing greater statistical power to assess noisy ecological patterns. These data sets also have the potential drawback of lacking the precision of researcher-generated data sets. As survey data do not attempt to control for the variability in agricultural systems, resulting data sets could harbor relatively high between-year differences in pest density, climatic conditions, insecticide applications, and landscape composition. Despite this possible lack of precision, in this study we were able to extract general and useful patterns with regards to landscape composition and *L. hesperus* density that are largely consistent with findings from experimental studies. Beyond this, the use of pre-existing survey data sets allowed us to expand the range of crop types considered and identify previously unevaluated crops as potentially important. Results from this study thus support the use of survey data to advance IPM at the landscape scale.

Conclusions

Land use within the San Joaquin Valley is shifting, moving away from an agricultural landscape dominated by cotton and alfalfa fields towards a suite of more profitable and cost effective crops. Cotton acreage has fluctuated strongly during recent decades, declining from 1.4 million acres in the 1980s to under 300 000 acres in 2008 (Goodell, 2009), and then increasing to 431 000 acres in 2011 (Cline, 2011). In recent years, the acreage of safflower has increased. The results presented here suggest that this shift in landscape composition would result in an increase in *L. hesperus* density in cotton. Indeed, in 2008, additional safflower acreage was thought to be the reason for extremely high *L. hesperus* densities in cotton, requiring multiple insecticide applications and resulting in substantial yield losses (Goodell, 2009; Carrière et al., 2012). The use of a large survey data set allowed us to examine a wide range of crops and explore their relationships to *L. hesperus*, whether it be positive, negative, or neutral. In doing so, crops were examined that are not prominent now, but may become important landscape features in the future. The enhanced statistical power and scope for investigation provided by large, consultant-derived data sets will likely be key factors in the future for understanding the dynamics of generalist pests in changing agroecosystems.

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Appendix A

Evaluating the possibility of pooling the data set across years

Because our data set covered 6 years (2003–2008), we hoped that more power for our inferences could be gained from pooling data across years and performing a global analysis. However, accurate analysis of pooled data requires comparable spatial autocorrelation across years. To test for among-year differences, we used a method and program called 'coregionalization analysis with a drift' (CRAD; Pelletier et al., 2009a,b). This method decomposes the spatial data into a deterministic component (drift), which does not contain the spatial autocorrelation but contains the spatial heterogeneity of the mean, and a random component, composed of a spatially autocorrelated part and a non-spatial (purely random) part. The relative importance of the deterministic component, the spatially autocorrelated part of the random component, and the non-spatial part of the random component were quantified by a pseudo-variance (drift) and two 'real' variances, using the local drift estimation procedure L1 for the former (Pelletier et al., 2009a). The sum of the three variance components provides a good approximation of the total variance (Table A1). The results from this analysis demonstrated the presence of significant spatial autocorrelation in all of the years except 2003 and 2007 as well as drifts of varying importance over years, strongly suggesting that pooling across years and conducting a global analysis would not be appropriate.

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Table A1 Decomposition of the total variance in *Lygus hesperus* densities each year from 2003 to 2008, by application of the method of coregionalization analysis with a drift (phase I). The resulting variance components are: a pseudo-variance for the deterministic component (drift) and two 'real' variances for the spatially autocorrelated component and a non-spatial component

Deterministic component		Random component		
Year	Drift	Spatially autocorrelated part[1]	Non-spatial part	Total variance
2003	0.777	0 (N/A)	0.315	1.092
2004	0.101	0.105 (7170 m)	0.187	0.393
2005	0.148	0.153 (1945 m)	0.093	0.394
2006	0	0.319 (4611 m)	0.131	0.450
2007	0.091	0 (N/A)	0.075	0.166
2008	0.070	0.119 (5450 m)	0.078	0.267

[1] Distances in parentheses are the ranges of spatial autocorrelation when its presence was detected.