



Detecting pest control services across spatial and temporal scales



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ABSTRACT

Natural habitat may deliver ecosystem services to agriculture through the provision of natural enemies of agricultural pests. Natural or non-crop habitat has strongly positive effects on natural enemies in cropland, but the resulting impact on pests is not as well established. This study measured weekly natural enemy (syrphid fly larvae) and pest (cabbage aphid) abundances in Central California broccoli fields for three years. Abundance of syrphid fly larvae increased strongly with the proportion of natural habitat surrounding the farm. As the density of syrphid fly larvae increased, weekly aphid population growth rates slowed, such that aphid densities just prior to harvest were lowest in farms with natural habitat. These landscape-mediated impacts of syrphids on aphids were not evident when data were aggregated into annual averages, a common metric in research on pest control services. We suggest that higher temporal resolution of data for natural enemy and pest abundance can reveal top-down control that is otherwise masked by seasonal and interannual variation in environmental factors.

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1. Introduction

Natural enemies, the predators and parasitoids of agricultural pests, provide a valuable ecosystem service to agriculture through reduction or control of pest populations. Yet the magnitude of top-down control operating in managed ecosystems and the extent to which these dynamics are influenced by farm and landscape characteristics is not always clear, hindering more accurate assessments of the importance and value of trophic ecology in food production. Natural enemies may forage far beyond farm boundaries and rely on nearby natural habitat. Understanding the full picture of predator-prey relationships therefore requires a landscape-scale perspective (Tscharntke et al., 2007). Despite a well-established trend of natural enemy diversity and abundance increasing in response to landscape-level habitat complexity, pest abundance does not show as strong or as consistent a response (Chaplin-Kramer et al., 2011b). This apparent lack of a generalizable trend suggests either that top-down control is not operating in these systems, or that the level of control that exists is undetectable by common sampling methods. Our study uses detailed analyses of pest and natural enemy densities across space and time to examine the relationship between natural habitat, trophic dynamics, and pest control services.

The challenge in detecting pest control services lies in differentiating the role of natural enemies from that of many other variables that can influence pest distributions, such as climate, host plant presence, resource concentration and dispersal patterns (Rusch et al., 2010), when all can vary across a landscape gradient. Many studies investigating landscape effects on pest control take only a snapshot of pest and enemy densities at one point during the season, or combine multiple samples into one average or cumulative measure, or limit their study period to one year (Chaplin-Kramer et al., 2011b). When population growth is measured, it is often between only two time periods during the season (Rand and Tscharntke, 2007; Roschewitz et al., 2005; Thies et al., 2005, 2011). Such measurements may not provide the temporal resolution needed to document pest control that is actually occurring, which could account for the disconnect between the positive effects of landscape complexity on natural enemy communities and the absence of a concomitant effect on pest communities and pest control (Tylianakis et al., 2006). Indeed, the few studies analyzing multiple samples over a season and/or over multiple years have emphasized the importance of incorporating seasonal and interannual variation in their analyses (Dib et al., 2010; Menalled et al., 2003; Oberg et al., 2008; Östman et al., 2001; Prasifka et al., 2004; Romeu-Dalmau et al., 2012; Schmidt and Tscharntke, 2005a). Therefore, it may be necessary to compare population growth trajectories rather than simply abundances, to elucidate the role of natural enemies in controlling pest populations that vary endogenously in space and time.

Here, we investigate the role natural habitat plays in the population dynamics of cabbage aphids (*Brevicoryne brassicae*) and their syrphid predators (Diptera: Syrphidae) in broccoli (*Brassica*

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oleracea, var. *italica* cv. Gypsy). By analyzing weekly insect samples taken over three years across a landscape gradient, we explore how population densities of pests and predators change over time and space. Specifically, our goal was to determine the impact of landscape complexity on: (1) syrphid communities, (2) aphid densities on the crops throughout the growing season and just prior to harvest, and (3) suppression of aphid population growth by syrphids. We suggest that this form of analysis is necessary to accurately quantify pest control services that may otherwise be masked by endogenous variation of pest population dynamics.

2. Materials and methods

This research was conducted in California's Central Coast region, where nearly half of the broccoli produced in the US is grown. Cabbage aphids are a major pest of broccoli and are prey for a number of natural enemies, including parasitic wasps (*Diaeretiella rapae*), lady beetles (Coccinellidae), lacewing larvae (Chrysopidae), spiders, and a variety of other coleopteran and hemipteran predators. However, the larvae of flies in the family Syrphidae are the most abundant aphid predator by far in this system (70% of all natural enemies were syrphids, across all sites in all three years; unpublished data). It has been suggested that syrphids may in fact be the most efficient predators of the cabbage aphid (Van Emden, 1963). Adult syrphid flies are extremely mobile, searching in many different habitats for nectar and pollen on which to feed, in order to obtain the energy necessary for reproduction (Almohamad et al., 2009; Schneider, 1969). Syrphids also rely on perennial habitats for alternate (non-crop) prey for their larvae when crop aphid populations are low, shelter from strong wind that would otherwise prevent their flying, and possibly overwintering habitat (Bugg et al., 2008). Aphidophagous syrphid flies are therefore an excellent study taxon to use to explore the effects of landscape on pest control.

The study was conducted on 24 organic broccoli farms in Santa Cruz, Monterey, and San Benito Counties during the summer growing seasons of 2006–2008. Due to the annual rotation schedules of these farms, different fields were used each year, and new sites were acquired to replace producers that did not grow broccoli in a given year. Ten farms were sampled in all three years, and 14 in at least two years, for a total of 15 farms in 2006, 16 in 2007, and 17 in 2008. The landscapes in which the farm sites were set spanned a gradient ranging from less than 5% to more than 80% natural habitat within 1, 2, and 3 km radii of the farm. Natural habitat was composed predominantly of grassland, shrubland, and woodland. Most of the farms were large-scale monoculture industrial organic operations, similar in most respects to conventional farms except for the restrictions on use of pesticides and synthetic fertilizers. The few farms that grew a more diverse array of vegetables in smaller quantities occurred on both ends of the landscape gradient (as experimental or demonstration farms; with 3%, 6% and 10% natural habitat within 3 km of the farms on the simple end of the landscape gradient, and 66%, 77% and 87% natural habitat on the complex end).

Geographic information (point data) was taken at the center of each sampling transect each year using a Global Positioning System (Trimble Geo XT), and imported into Geographic Information Systems (ArcGIS, Version 9.3.1, Environmental Systems Research Institute). Aerial photographs of 1 m resolution were obtained through the National Agricultural Imagery Project (<http://gif.berkeley.edu/resources/naip.html>) for the 3 km area surrounding each farm site in each year. The photographs were digitized using an object-based image analysis program called eCognition (version 5.0, Definiens Inc., Alexandria VA), and the resulting maps were classified by hand into different land-uses (natural habitat, including all habitat types listed above;

agriculture; residential; urban or industrial; water). The proportional area of natural habitat was then computed at a radius of 0.5, 1, 1.5, 2, 2.5, and 3 km around the farm site using Hawth's Tools (version 3.27, <http://www.spatial ecology.com>). The proportion of natural habitat was used as a metric of landscape complexity in subsequent analysis, with higher proportions of natural habitat around the farm signifying greater landscape complexity.

2.1. Arthropod collection

Ten broccoli plants per week were collected at each field site starting four to seven weeks before harvest and continuing every week until harvest. The variation in total weeks sampled occurred because the crops occasionally reached maturity more quickly or slowly than the grower's anticipated schedule. Further, different growers had different planting schedules, and as a result the first week of sampling occurred anywhere between May and August across the study sites. The variable planting dates were unavoidable due to studying many different farms in different locations. However, there was no significant correlation between sampling date and farm placement within the landscape gradient, and sampling date was included as a potential explanatory variable in the analysis.

Individual plants and the insects they harbored were collected every 5 m along a 50 m transect for a total of 10 plants per site. Transects started from the edge of a field with no weeds or insectary plantings wherever possible, to standardize edge effects in different-sized fields (Kremen et al., 2004). Entire plants were cut at the base and immediately placed in individual sealed plastic bags, and each plant was washed over a sieve to remove and collect insects within 48 h of return to the lab. This collection technique ensured that all syrphids inhabiting a plant were detected, as syrphid larvae are primarily nocturnal, hiding in the folds of leaves during the day (Rotheray, 1986), and may therefore be underestimated by visual observation in the field.

2.2. Arthropod abundance, composition and diversity

Arthropods were identified to species or family level under a dissecting microscope. Different syrphid species are difficult to distinguish as larvae, so a sub-sample of those collected in 2007 (355 individuals from 14 farms sampled over the course of the season) were reared through pupation to determine the composition and estimate the diversity of the community. Larvae were collected at all field sites, but only 14 sites were included in the analysis because no individuals completed development at the remainder of the sites. A total of 700 larvae were collected; 331 suffered mortality during rearing or arrested development in pupation, and 14 had been parasitized, resulting in a sample of 355 larvae that completed development and could be identified. The labor-intensiveness of the rearing process limited the ability to conduct this aspect of the study across multiple years; therefore no temporal effects are captured in the measures of arthropod composition and diversity. This additional information is meant merely to complement the more rigorous examination of abundance, by considering how different species may respond to complexity at different spatial scales. Upon rearing it became evident that syrphid eggs could not be reliably differentiated from leafminer eggs (*Liriomyza* spp., Diptera: Agromyzidae), so only larval counts were used in these analyses.

2.3. Analysis

Data were analyzed in the statistical program R (version 2.13.2, <http://cran.R-project.org>, packages nlme and qpcR), using Akaike Information Criteria corrected for small sample size (AICc), and AICc weights as a basis of model selection; summary weights were also

calculated for each variable using model averaging (Burnham and Anderson, 2002). Parameter estimates were derived for the top four models in each analysis, using linear mixed-effects models with repeated measures incorporated by designating site as a random effect. All models were examined first as a univariate relationship between the variable of interest and the proportion of natural habitat at six different scales (0.5–3 km) around the farm in order to determine which scale to use in subsequent multivariate analyses (using the lowest AICc score to select the best scale, Table S1 in the online supporting materials). Insect counts were natural log-transformed and first analyzed for edge effects along the transects; since none were detected, the counts on individual plants were averaged over the ten plants collected at each site in each week.

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.10.007>.

Estimates of syrphid diversity (measured by richness and Shannon's diversity index) and the relative abundance of each syrphid species in comparison to the others were based on the rearing sub-sample of 2007. Syrphid diversity and relative abundance were analyzed in simple linear models with the proportion of natural habitat surrounding the farm at different scales.

Weekly mean syrphid densities (ln syrphid larvae/plant for each week, S_w) were analyzed in linear mixed-effects models, with several possible fixed effects: proportion of natural habitat, local site complexity (categorically defined as monoculture or diverse, as described in Study System, above), year (tested as a categorical factor, since there were only three years), planting date, week until harvest, and aphid density (ln aphids/plant for the same week, $A_{w(t)}$). These syrphid data were also lumped into season-wide averages (ln syrphid larvae/plant for each year, S_y) and analyzed with landscape complexity as a predictor variable, an approach more typically taken in the literature. This season-wide average analysis employed a simple linear model rather than a mixed-effects model because no repeated measures were taken; even when farms were sampled in more than one year, the fields sampled occurred at different sites with different proportions of natural habitat each year.

Weekly mean aphid densities (ln aphids/plant for each week, A_w) and two additional response variables related to aphid densities, final aphid density (A_f) and changes in aphid density from one week to the next (ΔA) were analyzed in linear mixed-effects models similar to those for syrphids. The mean number of aphids per plant in the week before harvest, A_f , presents a management-relevant measure of pest loads in a season. Aphids rarely cause enough damage to broccoli to impact yield, but they do pose a cosmetic problem for producers if they remain on the plant after harvest. Aphids that inhabit the space between the florets on a mature broccoli head are nearly impossible to remove through washing. Such produce will command a lower price or, in extreme infestation, will not even be harvested; this metric therefore provides the closest approximation to pest "damage," in the sense that it is inversely related to revenue. In contrast, ΔA provides a more thorough view of the seasonal aphid population dynamics, measured as:

$$\Delta A = \frac{\text{aphids per plant in week } (t)}{\text{aphids per plant in week } (t-1)}$$

The analysis of the natural log-transformed weekly aphid density metrics (ln A_w and ln ΔA) included proportion of natural habitat, local site complexity, year, planting date, week until harvest, and previous week's syrphid density ($S_{w(t-1)}$). The previous week's rather than the current week's syrphid density was used in the aphid analyses because the change in aphids from one week to the next is expected to be predominantly driven by the syrphids already present rather than those that arrive over the course of the week. The analysis for A_f included the same variables, with

the exception of week until harvest, which was not relevant for a measure of final densities.

As with the syrphid data, a linear analysis was performed on season-wide averages of aphid densities (ln aphids/plant for each year, A_y) with landscape complexity and season-wide syrphid densities in the same year ($S_{y(t)}$) as predictor variables.

3. Results

The most common species in this study system was *Allograpta obliqua* (accounting for 67% of all syrphids reared), but other species included *Sphaerophoria sulphuripes* (18%), *Eupeodes fumipennis* (6%), *Syrphus opinator* (4%), *Platycheirus steganius* (2%), *Toxomerus occidentalis* (1%), *Eupeodes volucris* (1%), and *Allograpta exotica* (<1%). Syrphid diversity was positively correlated with natural habitat at all scales, but the relationship was stronger and only significant at smaller spatial scales (0.5–1.5 km for richness, 0.5 and 1 km for Shannon diversity; Fig. 1a). In contrast, the abundance of the most common syrphid, *A. obliqua*, was more strongly correlated with natural habitat at larger scales, and only significant at 2.5 km. Average syrphid density over the whole growing season (S_y) was highly and significantly correlated with natural habitat at all scales ($p < 0.001$), and this relationship was likewise strongest at 2.5 km (Fig. 1b).

The landscape scale of 2.5 km also resulted in the strongest relationship between natural habitat and weekly syrphid densities (S_w). Natural habitat, aphid densities, and week (until harvest) all increased syrphid densities and all appeared in the top four models; one of the top two models included year as well (Table 1a, Table S1a in the online supporting information). Of these factors, natural habitat had the greatest impact on weekly syrphid densities.

Averaging aphid density over the whole growing season (A_y) did not reveal a significant effect of natural habitat at any scale (Fig. 1b). The most predictive spatial scale for the effect of natural habitat on weekly aphid densities (A_w) and final aphid densities (A_f) was 1–1.5 km, but all scales below 3 km performed relatively similarly (Table S1b and c). Year was the dominant factor in the models for A_w and A_f , with 2006 characterized by much lower aphid densities than 2007 or 2008 (45 ± 6 vs. 260 ± 55 and 311 ± 56 , respectively; mean \pm standard error). A_w also increased over the season (weeks until harvest; Table 1b). Both A_w and A_f responded to local site complexity, with fewer aphids on monocultures, and A_f was negatively correlated with natural habitat (A_w exhibited a similar trend, but this was not significant; Table 1b and c, Fig. 2). Syrphid densities (from the week prior to the final week before harvest) and planting date were not significant predictors of A_f .

In contrast, syrphid densities were the only significant explanatory variable for ΔA (Table 1d and Fig. 3), with greater declines or lower increases in aphid populations associated with more syrphid larvae present in the previous week. Local site complexity and natural habitat were included along with syrphid density in high-ranked models, but these were not significant effects (Tables 1d and S1d). Week, year, and planting date were also not significant.

4. Discussion

In this study, lower aphid population growth was associated with the more abundant syrphids found on farms embedded in more natural landscapes, despite substantial interannual variation in aphid densities. The season-wide or annual averages presented here for syrphid and aphid response to landscape complexity are representative of broader effects documented in the pest control literature (Chaplin-Kramer et al., 2011b; Letourneau et al., 2012; Werling et al., 2011; Woltz et al., 2012). Natural enemy response to natural habitat was strong (Fig. 1a), but no relationship was found between pest and predator or pest and natural habitat when cumulative measures such as annual averages were used (Fig. 1b). The relationship between landscape complexity or composition and aphids has been particularly difficult to resolve in the existing literature; although higher aphid predation or suppression of aphid population growth at the cage level has been demonstrated in more complex landscapes (Chaplin-Kramer and Kremen, 2012; Gardiner et al., 2009; Östman et al., 2001; Winqvist et al., 2011; Woltz et al., 2012), there is not always corresponding support for reduced aphid densities at the field level (Caballero-Lopez et al., 2012; Gagic et al., 2011; Jonsson et al., 2012; Rand and Tschamtkke, 2007; Roschewitz et al., 2005; Thies et al., 2005, 2011). This study demonstrates the importance of examining pest dynamics across temporal scales, from multiple measures within a year to multiple years within a study, in order to detect effects of natural enemies

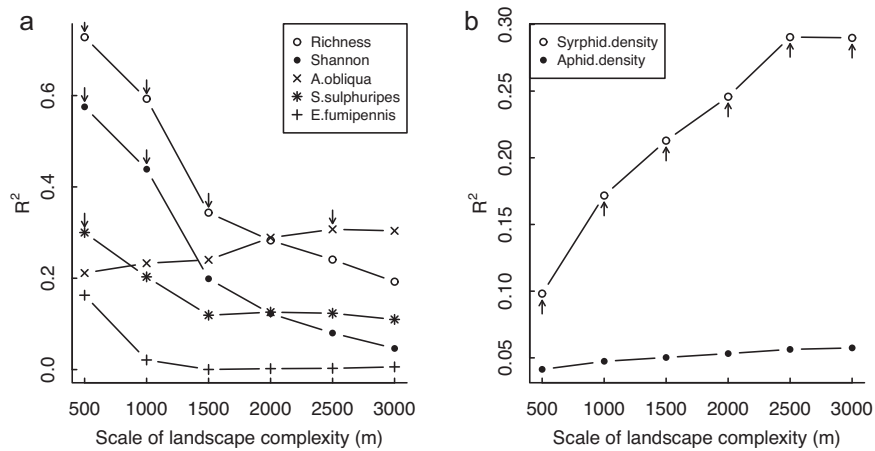


Fig. 1. Coefficient of determination (R^2) for the relationship between landscape complexity at different scales and (a) different indices of syrphid diversity or relative abundances of the most common syrphids (*A. obliqua*, *S. sulphuripes*, and *E. fumipennis*), and (b) annual average densities of syrphids and aphids over the whole growing season (individuals per plant, A_y and S_y). Significance at $p < 0.05$ is denoted with an arrow. Panel (a) is based on 2007 data only, the only year in which syrphid species were identified based on a rearing sub-sample. Average syrphid densities in panel (b) are calculated from the entire 3-year dataset.

Table 1

Fit of the models for syrphid and aphid densities, ranked by AICc weights, with the best models listed first. The full balanced sets of models tested ($N=63$, each variable entered into 32 models) can be seen in the online supporting information, Tables S1a–d. Model numbers correspond to models found in the supporting information, for predicting (a) weekly syrphid densities (S_w), (b) weekly aphid densities (A_w), (c) final aphid densities (A_f), and (d) weekly change in aphid densities (ΔA). All models listed fell above a threshold AICc weight of ≥ 0.05 (with weights reaching as low as 10^{-6} to 10^{-23} for the full model set). *Landscape complexity* measures % natural habitat within the most predictive scale (2.5 km radius for syrphids, 1 km radius for aphids), *Local complexity* is a categorical variable (simple versus complex), $\ln(S_{w(t-1)})$ is the previous week's mean syrphid larvae densities, *Week* is the time until harvest, and *Site* was included in all models as a random effect. Mean \pm standard errors and significance ($*p < 0.05$, $**p < 0.01$, $***p < 0.0001$) are given for the coefficients of each linear mixed effects model.

(a) $\ln(S_y)$	Weight	M49	M28	M58	M44
Landscape	0.999	1.11 \pm 0.21***	-1.18 \pm 0.22***	1.06 \pm 0.21***	1.12 \pm 0.23***
Local [Monoculture]	0.157	-0.11 \pm 0.12*		-0.14 \pm 0.13*	
$\ln(A_w)$	0.999	0.21 \pm 0.03***	0.19 \pm 0.03***	0.21 \pm 0.03***	0.18 \pm 0.03***
Year [2007]	0.591	-0.29 \pm 0.14**		-0.29 \pm 0.14**	
Year [2008]	0.591	-0.44 \pm 0.14**		-0.42 \pm 0.14**	
Week	0.982	0.09 \pm 0.02***	0.11 \pm 0.02***	0.10 \pm 0.02***	0.11 \pm 0.02***
Δ AICc		0.646	3.700	3.786	
AICc weights		0.475	0.344	0.075	0.072
(b) $\ln(A_w)$	Weight	M46	M36	M53	M58
Landscape	0.547	-0.81 \pm 0.55		-0.68 \pm 0.58	
Local [Monoculture]	0.853	-0.82 \pm 0.31**	-0.71 \pm 0.30*	-0.80 \pm 0.31*	-0.88 \pm 0.32*
$\ln(S_{y(t-1)})$	0.239	-0.22 \pm 0.15		-0.18 \pm 0.15	
Year [2007]	0.996	1.42 \pm 0.34**	1.50 \pm 0.34***	1.43 \pm 0.35***	1.38 \pm 0.35**
Year [2008]	0.996	1.65 \pm 0.34**	1.72 \pm 0.34***	1.67 \pm 0.35***	1.63 \pm 0.35**
Week	0.997	0.32 \pm 0.06***	0.32 \pm 0.06***	0.35 \pm 0.06***	0.34 \pm 0.06***
Δ AICc		0.629	2.702	2.750	
AICc weights		0.345	0.252	0.089	0.087
(c) $\ln(A_f) \sim$	Weight	M17	M8	M11	M4
Landscape	0.822	-1.42 \pm 1.65*		-1.12 \pm 0.66*	
Local [Monoculture]	0.721	-0.80 \pm 0.37*		-0.62 \pm 0.38	
$\ln(S_{y(t-1)})$	0.199				
Year [2007]	0.999	1.98 \pm 0.41***	1.99 \pm 0.43***	2.09 \pm 0.43***	2.08 \pm 0.44
Year [2008]	0.999	1.63 \pm 0.41***	1.58 \pm 0.42***	1.74 \pm 0.42***	1.68 \pm 0.43
Δ AICc		1.716	3.033	3.077	
AICc weights		0.433	0.184	0.095	0.093
(d) $\ln(\Delta A) \sim$	Weight	M3	M12	M8	M22
Landscape	0.281	0.24 \pm 0.34		0.16 \pm 0.34	
Local [Monoculture]	0.349	-0.29 \pm 0.19		-0.27 \pm 0.19	
$\ln(S_{y(t-1)})$	0.999	-0.74 \pm 0.11***	-0.80 \pm 0.12***	-0.77 \pm 0.12***	-0.82 \pm 0.13***
Δ AICc		1.260	1.921	3.444	
AICc weights		0.391	0.208	0.150	0.070

and landscape complexity. The response of aphids in this system to their syrphid enemies at the field level could only be detected at

the finer temporal resolution of weekly data. Further, factoring in strong annual and local site effects revealed a negative relationship

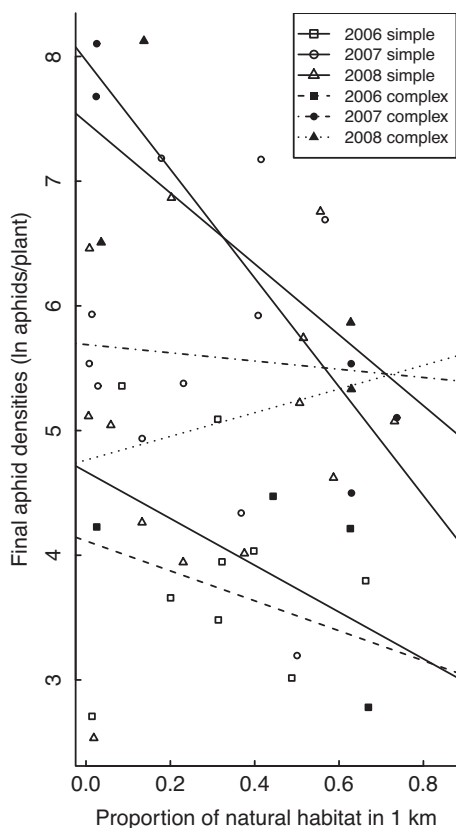


Fig. 2. Mean final aphid densities ($\ln(A_T)$) as a function of landscape complexity (proportion of natural habitat) within a 1 km radius, year and local site complexity (simple monoculture or diverse).

between natural habitat and aphid densities in the week before harvest that would not have been evident in any single year (Table 1c and Fig. 2).

The importance of seasonal and interannual variation found here has also been emphasized in other studies (Dib et al., 2010; Menalled et al., 2003; Prasifka et al., 2004; Romeu-Dalmau et al., 2012; Schmidt and Tschamtkke, 2005b; Tylianakis et al., 2006), but understanding the factors behind such temporal variation in pest densities remains a major challenge. Aphid densities were orders

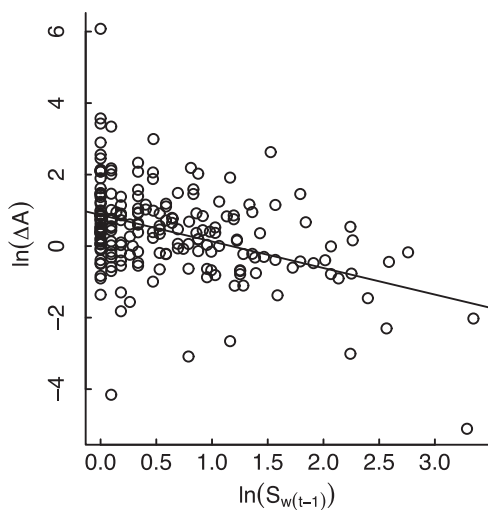


Fig. 3. Change in mean aphid densities from one week to the next ($\ln(\Delta A)$) against the previous week's (first of the two weeks being compared) mean syrphid larvae densities ($\ln(S_{w(t-1)})$).

of magnitude higher across all sites in 2007 and 2008 than in 2006, a year with an unusually long wet season (heavy rains through May). Rain prevents winged aphids from dispersing, and increased rainfall is associated with delayed aphid establishment (Thackray et al., 2004). Rain can also impact aphid survival, knocking them off plants, leading to mortality from impact, starvation, or ground-dwelling predators (Hughes, 1963; Winder, 1990). The late rains in 2006 may have contributed to delayed aphid establishment in the crops and ultimately prevented aphid populations from ever reaching their peak (Dixon, 1977). Indeed, 2007 and 2008 populations showed a distinct peak around mid to late July, while aphids in 2006 showed no real trend with season (Chaplin-Kramer, 2010). Despite these dramatic differences in aphid densities from year to year, weekly aphid population changes were best explained by syrphid densities alone (Fig. 3); the relationship between predator and pest was not improved by incorporating interannual variation (Table 1d). In contrast, final aphid densities did not respond to syrphid densities, and only responded to landscape complexity when year was included as a covariate (Table 1c); the season-wide average aphid densities showed no response to landscape at any scale (Fig. 1b). Population change may therefore be a more reliable way of detecting pest control services than snapshot or cumulative metrics of aphid densities (Chaplin-Kramer et al., 2011b).

Another problem in detecting an effect of natural habitat on pest densities, and a reason why population change may provide a better indication of pest control services than population densities, is that landscape features may impact pests in conflicting ways. The indirect effects of natural habitat on pests (via natural enemies) may be augmented or diminished by a variety of competing direct effects. On the one hand, natural habitat embedded in agricultural landscapes may act as barriers to pest dispersal from one crop field to another (Lewis, 1965; Pasek, 1988; Schmidt and Tschamtkke, 2005a) or may interfere with pests locating their host crops by reducing the resource concentration of monoculture cropping (Root, 1973). On the other hand, the same resources provided by natural vegetation that benefit parasitoids and predators could also benefit some pests, especially lepidopterans that seek nectar as adults (Winkler et al., 2009), and natural habitat could also serve as a perennial refuge for pests, from which to continually recolonize annual crop fields (Pasek, 1988). The presence of alternate hosts in complex landscapes has been shown to be a counterbalancing force to increased top-down control, in aphids in particular (Roschewitz et al., 2005; Thies et al., 2005). In our system, the Mediterranean climate means that aphids do not need to overwinter (Hughes, 1963), but they may build up populations on the weedy mustard that commonly occurs in unmanaged habitats near agricultural fields (Chaplin-Kramer et al., 2011a).

The positive response of natural enemies to natural habitat in this system was robust, significant at all scales measured (from 0.5 to 3 km; Fig. 1b). The fact that all farms studied were organic suggests that syrphids were indeed responding to natural habitat, and not to pesticide intensity, which often covaries with landscape complexity and may be a stronger force driving natural enemy abundance (Hendrickx et al., 2007; Jonsson et al., 2012). Natural habitat was most predictive of syrphid densities at one of the largest scales (2.5 km), while syrphid diversity responded most strongly at the smallest scale (0.5 km). It is likely that the pattern for syrphid densities was driven primarily by the abundance of the most common species (comprising two-thirds of all syrphids reared), *A. obliqua*, which also responded most strongly at the 2.5 km scale. Some of the other syrphid species responded at smaller scales, including the second most common, *S. sulphuripes*, confirming previous findings (0.5–1 km; Haenke et al., 2009). It is also possible that through their excellent vision and strong flying, syrphids can respond to resource opportunities at many different

scales (Schneider, 1969). Indeed, many syrphid species may be supported by even small grassland patches and scarce flower resources or hedges along fields (Jauker et al., 2009; Krause and Poehling, 1996), and syrphid richness can be responsive to spatial scales as coarse as 10–20 km (Keil et al., 2011). Mobility may be a key feature determining natural enemy effectiveness, as several exclusion experiments have shown greater impacts on pest populations by flying as compared to ground-dwelling natural enemies (Holland et al., 2008, 2012; Schmidt et al., 2003). Furthermore, though syrphids are not true generalists, most syrphid species can feed on a variety of aphid species. This breadth of diet may buffer them against environmental stochasticity and fluctuations in prey densities. Lack of strong fourth trophic level control (<10% parasitism of syrphids across all sites) may also stabilize the pest control provided by syrphids in this system, since there are no dampening effects of hyperparasitoids seen in other systems (Gagic et al., 2011; Rand et al., 2012). The strength of the relationship between natural habitat and syrphids across spatial scales suggests that they may be a fairly reliable provider of aphid control services. Replication of ecological functions across a range of scales can often lead to greater resilience of ecosystem services in the face of disturbance (Elmqvist et al., 2003).

5. Conclusions

Dynamic measurements such as pest population growth, especially as linked to natural enemy populations, may provide a valuable indicator of pest control services in addition to pest densities. Of course, natural enemy suppression of pest populations does not necessarily imply adequate pest control, which is determined by economic thresholds rather than ecological criteria. Natural enemies may suppress pest population growth without reducing pest densities (Thies et al., 2005), or they may indeed reduce pest densities but not reduce them enough to avoid plant damage. In either case, growers may find it hard to rely upon natural enemies as a sufficient means of pest control. It is nonetheless important to recognize and quantify the contribution that natural enemies make to an overall pest management program and to identify conditions that could increase that contribution (Kremen, 2005).

In this study, landscape complexity enhanced natural enemies, which slowed pest population growth at the field level, and reduced final pest densities amidst substantial interannual variation. Including several indicators of pest control services provided by natural enemies can help determine the degree to which natural habitat can provide this ecosystem service and identify potential reasons why the service may be diminished or ways that it may be enhanced.

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