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Landscape diversity and crop vigor outweigh influence of local diversification on biological control of a vineyard pest

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Abstract. The influence of local and landscape habitat diversification on biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn) by its key parasitoids *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *Anagrus daanei* Triapitsyn was studied in wine grape vineyards. At the landscape scale, *Anagrus* rely on alternative host species in non-crop habitats outside of the vineyard to successfully overwinter, while at the local scale vineyard diversification can provide resources, such as shelter and floral nectar, which improve parasitoid performance. In a two-year experiment, plots with and without flowering cover crops were compared in vineyards representing a gradient of landscape diversity. While the cover crops did attract natural enemies, their populations were unchanged in the crop canopy and there was no difference in parasitism rate, leafhopper density, crop quality, or yield. Vineyards in diverse landscapes had higher early-season abundance of *Anagrus* spp., which was linked to increased parasitism and decreased late-season populations of *E. elegantula*. Leafhopper densities were also positively associated with crop vigor, regardless of landscape or cover crops. Flowering cover crops did increase abundance of some natural enemy species as well as parasitism rate in vineyard landscapes with intermediate levels of diversity, indicating a local × landscape interaction, although this did not lead to reductions in *E. elegantula* densities. These findings indicate that, in this agroecosystem, landscape diversity mediates and in many ways outweighs the influence of local diversification and that *E. elegantula* densities were regulated by a combination of biological control and crop vigor.

Key words: *Anagrus;* cover crop; crop vigor; *Erythroneura;* floral resource provision; landscape diversity.

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INTRODUCTION

Agroecosystem simplification reduces biodiversity and associated ecosystem services, such as biological control of crop pests (Swift et al. 1996, Tilman et al. 2001). Biological control can be improved by increasing habitat diversity within the crop at the local scale (Andow 1991, Altieri 1999, Poveda et al. 2008, Letourneau et al. 2011) as well as outside the crop at the landscape scale (Landis et al. 2000, Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Veres et al. 2013). The relationship between habitat diversity and biological control is not, however, always consistent and outcomes are primarily determined by species-specific characteristics, such as dispersal capacity and overwintering habitat requirements (Duelli and Obrist 2003, Tscharntke et al. 2007). Moreover, the efficacy of on-farm diversification practices is likely mediated by landscape context itself (Batáry et al. 2011, Tscharntke et al. 2012, Jonsson et al. 2015). For example, in extremely

simplified landscapes provision of on-farm habitat may have no effect on natural enemies due to an inadequate meta-population (Hanski 1998), whereas in extremely diverse landscapes the effect of on-farm habitat is muted due to high levels of natural enemy migration into the crop from the surrounding landscape (Tscharntke and Brandl 2004, Tscharntke et al. 2005). Thus, it may be that on-farm diversification has the strongest effect on natural enemy abundance and impact in landscapes with intermediate diversity.

Pest densities can also be influenced by changes in crop vigor (White 1974, Mattson 1980, Price 1991). Abiotic stress can lead to increased availability of nitrogen in plant tissue due to reduced protein synthesis as well as negatively impact production of secondary metabolites associated with plant chemical defense mechanisms (White 1984, Mattson and Haack 1987). In both cases, plant hosts under such conditions are more preferred by and/or susceptible to attack by insect herbivores. Alternately, it has also been demonstrated that insect pests prefer overly vigorous plants or plant modules (Price 1991) since these tissues may have increased nutritional content (Inbar et al. 2001). The addition of non-crop habitat into an agroecosystem can potentially reduce crop vigor through increased competition (Ingels et al. 1994, Masiunas 1998). Alternately, at the landscape scale, changes in microclimate associated with crop proximity to large stands of natural habitat can also influence crop vigor (Nuberg 1998, Wilson et al. 2015*b*). Thus in addition to increased natural enemy populations or decreased pest colonization, habitat diversification can also impact pest densities by influencing crop vigor (Daane and Costello 1998, Rukazambuga et al. 2002).

The Western grape leafhopper (*Erythroneura elegantula* Osborn [Hemiptera: Cicadellidae]) is a key vineyard pest in California and the Pacific Northwest (Daane et al. 2013). In California, *E. elegantula* typically completes two generations per year, with peak adult flights occurring in April–May and again in July–August. Adults overwinter in a reproductive diapause, and new eggs are not deposited until spring when there is new grape foliage (Daane et al. 2013). Feeding by adult and nymphal stages leads to leaf stippling which can reduce fruit yield and quality; furthermore, late-season populations of *E. elegantula* adults pose a nuisance to workers harvesting the grapes. The key parasitoids of *E. elegantula* are *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *Anagrus daanei* Triapitsyn (Hymenoptera: Mymaridae) (Daane et al. 2013, Wilson et al. 2015*a*). These parasitoids attack the eggs of *E. elegantula* and other related leafhopper species. Grape leafhoppers are also attacked by a number of generalist predators, including soldier beetles (Cantharidae), green lacewings (*Chrysoperla* sp.), big-eyed bugs (*Geocoris* sp.), brown lacewings (*Hemerobius* sp.), convergent lady beetles (*Hippodamia convergens* [Guérin-Méneville]), damsel bugs (*Nabis* sp.), minute pirate-bugs (*Orius* sp.), hover fly larva (Syrphidae), and spiders, which are considered the dominant generalist predator (>90% of population) in vineyards (Costello and Daane 1995). Although generalist predators can have an impact on *E. elegantula* populations (Hanna et al. 2003), the *Anagrus* parasitoids are considered the primary biological control agent of this pest (Daane et al. 2013).

Populations of *E. elegantula* and *Anagrus* spp. in vineyards are largely driven by differences in their overwintering requirements. While *E. elegantula* overwinter as adults, both *A. erythroneurae* and *A. daanei* must seek out alternate leafhopper host species that overwinter as eggs on other plant species, commonly found in natural habitats outside of vineyards (Doutt and Nakata 1965, Lowery et al. 2007). As such, proximity to overwintering habitat has been shown to influence vineyard abundance of *Anagrus* spp. early in the growing season (Doutt and Nakata 1973, Murphy et al. 1996, Wilson et al. 2015*a*). During the season, vineyard monocultures can also be inhospitable to *Anagrus* spp. due to the lack of carbohydrate food source, for instance, floral nectar, which has been shown to limit the longevity and thereby reduce reproductive potential (English-Loeb et al. 2003, Segoli and Rosenheim 2013). Various habitat diversification schemes have been suggested to address this, including the use of annual cover crops (Ingels 1998, Dufour 2000). Studies evaluating the use of cover crops to enhance biological control of *Erythroneura* leafhoppers in vineyards have found either no change (Altieri and Schmidt 1985, English-Loeb et al. 2003) or decreased leafhopper densities in plots with a cover crop (Settle et al. 1986, Wolpert et al. 1993, Daane and Costello 1998, Roltsch et al. 1998, Nicholls et al. 2000, Costello and Daane 2003, Hanna et al.

2003). While some have concluded that the effect of cover crops on leafhoppers is mediated by increased natural enemy populations (Roltsch et al. 1998, Nicholls et al. 2001, Hanna et al. 2003), others suggest an additional or primary contribution to changes in vine vigor (Costello and Daane 2003). The influence of plant vigor or plant stress on insect performance varies by guild (Larsson 1989), with leaf mesophyll feeders in particular (such as *Erythroneura* leafhoppers) seeming to be more sensitive to such changes in plant quality (Koricheva et al. 1998, Huberty and Denno 2004). Studies across multiple cropping systems have demonstrated leafhopper response to changes in crop water stress (Leigh et al. 1974, Hoffman and Hogg 1992, Schowalter et al. 1999, Fornasiero et al. 2012) and nutrient levels (Coyle et al. 2010, Iqbal et al. 2011, Joern et al. 2012). More specifically, *Erythroneura* leafhoppers in vineyards prefer vines with increased nitrogen content (Daane and Costello 1998, Wilson et al. 2015*a*, *b*) and applied irrigation amounts (Trichilo et al. 1990, Daane and Williams 2003, Costello and Veysey 2012).

A number of studies have evaluated the use of cover crops to increase biological control in vineyards (Berndt et al. 2002, 2006, Danne et al. 2010, Simpson et al. 2011, Irvin et al. 2014) and of *Erythroneura* leafhoppers in particular (Wolpert et al. 1993, Daane and Costello 1998, Costello and Daane 2003, Hanna et al. 2003), although only a few have utilized flowering summer cover crops (Nicholls et al. 2000, English-Loeb et al. 2003). More recently, studies have begun to investigate the influence of landscape diversity on vineyard arthropods (Botero-Garcés and Isaacs 2004, Thomson et al. 2010, Hogg and Daane 2011, 2013, D'Alberto et al. 2012) and biological control of pests (Thomson and Hoffmann 2009, 2013) and specifically leafhoppers (Wilson et al. 2015*a*). Yet to date, no studies have investigated the interaction between local vineyard diversification practices and landscape diversity. For this reason, this study was designed to elucidate the relative influence of local and landscape diversity on biological control of *E. elegantula* in vineyards by comparing pest and natural enemy densities, vine vigor, and crop yield in paired plots with and without summer flowering cover crops over a two-year period (2012–2013) in multiple vineyards that represented a gradient of surrounding landscape diversity.

Methods

Study sites

Experimental blocks were in commercial vineyards >0.8 ha (2 acres) located in Napa and Sonoma County, California, United States. All vineyard blocks were located on level ground and consisted of vines that were at least five years old; cultivars were Cabernet Sauvignon (five sites), Zinfandel (two sites), and Merlot (one site). Each experimental block was comprised of 60 vine rows with 50–80 vines per row. Blocks were divided in half (i.e., two plots), and each plot was randomly assigned to either control or flowering cover crop treatment. In each plot, all samples were taken from the five middle vine rows. Within each of the five sample rows, no measurements were taken from the first or last 10 vines. There were eight sites in 2012 and two sites in 2013, with each site as a replicate containing a plot with and without the flowering cover crops.

The flowering cover crop treatment consisted of *Phacelia tanacetifolia* Benth. (purple tansy), *Ammi majus* L. (Bishop's flower), and *Daucus carota* L. (Queen Anne's lace) sown in combination to alternate row middles. These flower species were selected for use due to their overlapping bloom sequence (*P. tanacetifolia*, *A. majus*, and *D. carota* bloom April–May, May–June, and July–September, respectively), known ability to attract natural enemies (Hickman and Wratten 1996, Pontin et al. 2006, Sivinski et al. 2011), and compatibility with standard vineyard management practices, which requires that flowers receive no supplemental irrigation and can be sown in the fall. In October or November, row middles were tilled and then flowers sown 0.32–0.64 cm deep (1/8–1/4 inch) using a compact seed drill (Schmeiser Series 98, Selma, California, USA) followed by a ring roller (Schmeiser Till an' Pak, Selma, California, USA) to firm the soil. *Phacelia tanacetifolia* was sown at a rate of 2.2 kg/ha (2 lbs/acre), while *A. majus* and *D. carota* were sown at 0.56 kg/ha (0.5 lbs/acre). Flowers relied on seasonal rains (October–April) to establish. All flower seeds were purchased from commercial providers with the exception of *D. carota*, which was gathered by the authors (HW and AFM) from wild stands growing along the side of the road in Napa and Sonoma County in order to select for drought-tolerant *D. carota*

seed. In the spring, alternate rows of weedy vegetation were tilled under in both treatment and control plots, thereby leaving treatment plots with an alternating set of row middles sown to the flowering cover crops and control plots with an alternating set of row middles with resident weedy vegetation.

Throughout the study, no insecticides targeting leafhoppers or hemipteran pests were used at any of the study sites. Insecticides were applied at four of the eight sites in 2012 as part of a mandatory eradication program for the invasive European grapevine berry moth (*Lobesia botrana* Denis & Schiffenmüller [Lepidoptera: Tortricidae]; Cooper et al. 2014). These mandatory insecticide sprays for *L. botrana* consisted of non-contact diamides, insect growth regulators, and/or avermectin. All of these pesticides have low natural enemy toxicity and little to no impact on *E. elegantula* populations (Bentley and Varela 2015).

Landscape diversity metrics

Vineyards used in this study were located in low-, intermediate-, and high-diversity landscapes, representing a continuum of landscape diversity, which was quantified as the relative proportion of natural, non-crop habitat within 0.5 km based on extracting "rangeland cover type" from the CalVeg dataset (USDA 2013) using ArcGIS 10.1 (ESRI, Redlands, California, USA). There were 71 possible values for rangeland cover type, as described by Shiflet (1994). The total area of each cover type was calculated within a 0.5 km radius around each vineyard site. Cover types were then consolidated into five categories: "natural habitat," "agriculture," "development," "water," and "no data." The "natural habitat" category consisted primarily of riparian, oak woodland, and chaparral habitats, while the "agriculture" category was almost entirely vineyard. "Development" included all commercial and residential areas, including urban vegetative landscaping. For this analysis, "landscape diversity" is defined as the percentage of "natural habitat" within 0.5 km of the vineyard study site.

Insect abundance and parasitism rate

Natural enemy abundance on the cover crops.—Sweep-nets were used to monitor abundance of key generalist predators on ground covers in all plots. At peak bloom of each species of flowering cover crop, samples were collected from the flowers in the treatment plots and from the resident weedy vegetation in the control plots. Resident weedy vegetation primarily consisted of morning glory (*Ipomoea purpurea* [L.] Roth), spurges (*Euphorbia* spp.), cheeseweed (*Malva parviflora* L.), filaree (*Erodium* spp.), and knotweed (*Polygonum arenastrum* Boreau). Peak bloom of *P. tanacetifolia*, *A. majus,* and *D. carota* occurred on 22 April, 14 June, and 2 August in 2012 and on 20 April, 30 May, and 25 July in 2013, respectively. In each round of sampling, five sets of 30 sweeps each were collected from the ground covers in each plot using a 30.5 cm diameter sweep-net (7212HS, BioQuip Products, Rancho Dominguez, California, USA). Insects were transferred to plastic freezer bags and brought to the laboratory for identification.

Natural enemy and Erythroneura elegantula *adult abundance in the crop canopy.*—*Anagrus* wasps, key generalist predators, and *E. elegantula* adults were monitored with 16 × 10 cm yellow sticky-traps (Sticky Aphid/Whitefly Trap; Seabright Laboratories, Emeryville, California, USA) in the early season (24 April–6 June 2012, 12 April–22 May 2013) and late season (10 July–21 August 2012, 14 July–28 August 2013). These early- and late-season periods approximately coincided with the two peak adult flight periods for *E. elegantula* adults. In each plot at each vineyard, five yellow sticky-traps were randomly assigned to vines within a plot sampling area and hung in the vine canopy from a trellis wire. Traps were replaced approximately every two weeks.

Following Costello and Daane (1999), spiders were sampled from the vine canopy using a modified beat-sheet in September of each year (12 September 2012 and 15 September 2013), when abundance of mature spiders is generally highest. The beat-sheet consisted of a 1-m^2 cloth funnel that fed into a detachable 3.78-L (1-gallon) plastic bag. Samples were collected from five randomly selected vines in each plot at each vineyard site. Sampling involved holding the funnel beneath the vine canopy and vigorously shaking the vine for 30 s in order to dislodge spiders into the funnel and plastic collection bag. All spiders were brought to the laboratory where they were identified to family.

Leafhopper egg parasitism rate.—Parasitism of leafhopper eggs was determined by evaluating

30 grape leaves from each plot at each site following emergence of first-generation *E. elegantula* nymphs (~1–15 June). Leaves were collected by removing one leaf each from shoot nodes one to three from 30 randomly selected vines. Leaves were brought to the laboratory and inspected with a dissecting microscope. Egg status was determined by the type of emergence mark present—a small slit in the egg close to the leaf surface indicated that *E. elegantula* had successfully emerged, whereas a circular hole on the top of the egg indicated emergence of an *Anagrus* wasp. Unemerged eggs were not included in the parasitism assessment, as their status could not be consistently determined.

Crop vigor, yield, and quality

Crop vigor was measured in all vineyard plots by total petiole nitrogen (N) content (%) at peak grapevine bloom in 2012 and 2013 as well as by cane pruning weights collected after the 2012 and 2013 growing seasons. Peak grapevine bloom was defined as >80% of grape clusters in full bloom. On 24 May–8 June 2012 and 22–29 May 2013, petioles were collected from 60 randomly selected vines in each plot at each site (one petiole per vine). A range of dates is given because peak grapevine bloom occurred on different dates depending on grape cultivar and local environmental conditions. Following Reisenauer (1978), each petiole was taken from opposite flower clusters near the base of a shoot. Petioles were brought to the laboratory, washed with deionized water, and dried at 55°C for 24 h. Samples were then sent to the University of California Division of Agriculture and Natural Resources Analytical Laboratory to quantify total N levels. Cane pruning weights were collected and weighed from 10 randomly selected vines in each plot in December and January following that years' experiment.

Crop yield and quality (°Brix) were determined by sampling 10 randomly selected vines per plot approximately 1–3 d prior to harvest. On each vine, all grape clusters were removed and weighed in order to quantify average cluster weight per vine per plot. After taking weights, crop quality was evaluated by measuring °Brix from three composite samples that consisted of 10 clusters each (one cluster from each of 10 vines).

Statistical analysis

Data aggregation and summary.—Data from the five yellow sticky-traps in each plot were averaged for each sample date within the early- and late-season periods. Data for each sample date were then converted to the number of organisms per day to account for differences in the length of each sample date, which ranged from 11 to 20 d. Since *Anagrus* populations can exhibit a rapid, density-dependent response to *E. elegantula*, data from only the first sample date in the early season were used as the measure of early-season *Anagrus* densities. Peak *E. elegantula* densities in the early- and late-season periods were determined by selecting the sampling date with the highest density of *E. elegantula* per trap per day in each period. Generalist predator data were separately summed across all sample dates within the early- and late-season periods. Data from the five beat samples of the vine canopy in each plot at each site were summed for each year of the study, resulting in one measure per plot per year.

Calculating natural enemy evenness.—Community evenness was separately quantified for generalist predators on the sticky-traps in both the early- and late-season periods as well as for spiders from the beat sampling by calculating Pielou's J ($J = H'/\ln(S)$) using the "vegan" package (Oksanen et al. 2015) in the statistics program R version 3.0.3 (R Core Team 2016). This was derived by first calculating the Shannon-Weaver index (H'): $H' = -\sum (P_i \times \ln P_i)$, where P_i is the fraction of the entire population made up of species i, and then dividing H' by the logarithm of species richness (S). J falls in a range of 0–1, with higher values representing a more even community.

Mixed-effects models.—Data on pest and natural enemy densities as well as total petiole N content were evaluated using linear mixed-effects models with Gaussian distribution and identity-link function. Parasitism data were evaluated by logistic regression using a generalized linear mixed-effects model with binomial distribution and log-link function. Both analyses were conducted with the "lme4" package (Bates et al. 2015) in R. Partial correlation values were calculated using the "r2glmm" package (Jaeger et al. 2016). Data from both years of the study were pooled, and therefore, all analyses included "site" as a random effect. To improve normality, all data on insect densities were $\log(x + 1)$-transformed and the log

Table 1. Factors effecting *Anagrus* (n = 20) and *Erythroneura elegantula* densities (n = 18) and parasitism rate (n = 18) during the early- and late-season periods.

Response	Main effect	Early season	Late season
Anagrus density	*E. elegantula* density	6.70**	35.90***
	Flowering cover crop	6.40**	0.20
	Landscape diversity	8.67***	0.20
E. elegantula density	*E. elegantula* density (early season)	. . .	8.91**
	Parasitism rate (early season)	. . .	(5.23)*
	Flowering cover crop	0.01	0.00
	Landscape diversity	0.65	1.28
	Total petiole nitrogen content	1.45	9.92**
Parasitism rate	*Anagrus* density	1.80	. . .
	E. elegantula /*Anagrus* ratio	7.66**	. . .
	E. elegantula density	3.17	. . .
	Flowering cover crop	0.42	. . .
	Landscape diversity	2.15	. . .

Note: Table shows χ^2 values from mixed-effects models.
$^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

odds transformation was used for petiole total N content (a percentage). Model comparison (χ^2 tests) was used to evaluate the influence of main effects against a reduced (null) model.

Analysis of early- and late-season generalist predator densities and evenness included the main effects "landscape diversity," "ground cover type" (i.e., presence or absence of the flowering cover crop), and "*E. elegantula* density" (i.e., peak densities during the early- or late-season periods, accordingly). Analysis of spider family abundance and evenness included the main effects "landscape diversity," "ground cover type," and "late-season *E. elegantula* density." Early- and late-season *Anagrus* and *E. elegantula* densities and parasitism rates were evaluated against a number of factors (see Table 1 for a summary of all main effects).

Landscape mediation of flowering cover crop effects was analyzed by evaluating whether or not differences in insect densities and parasitism rates between plots with and without flowering cover crops were more or less pronounced in certain landscapes. For each response variable tested, the difference between the treatment and control plot at each site was calculated for all sites, and then, these differences were evaluated with a model that included both a linear and non-linear term (i.e., a quadratic, second-order polynomial) for the main effect "landscape diversity." Analysis of organisms collected from the ground covers included "species of flower in bloom" and "site" as random effects. Analysis of variables from the vine canopy included "period" (i.e., early or late season) and "site" as random effects, with the exception of spiders and parasitism rate, which only included "site" as a random effect since they were sampled once per season.

Due to uneven sampling across all plots and sites in both years of the study, the number of complete cases varied in each analysis depending on which main effects were included in the model being evaluated. Sample size is therefore indicated for each analysis.

Results

Generalist predator abundance and evenness on ground covers

There were more *Orius* sp. and spiders on all three species of flowering cover crop as compared with resident ground cover vegetation in control plots, and there were more *Chrysoperla* sp. on *P. tanacetifolia* and *A. majus* and more *H. convergens* and *Nabis* sp. on *A. majus* (Fig. 1, Table 2). Natural enemy evenness was higher on *D. carota* (Table 2). Landscape diversity had no effect on natural enemy abundance or evenness on the ground covers (Table 2).

Generalist predator abundance and evenness in the crop canopy

Early-season predator populations in the crop canopy were mostly unaffected by the presence of flowering cover crops, with the exception of *Orius*

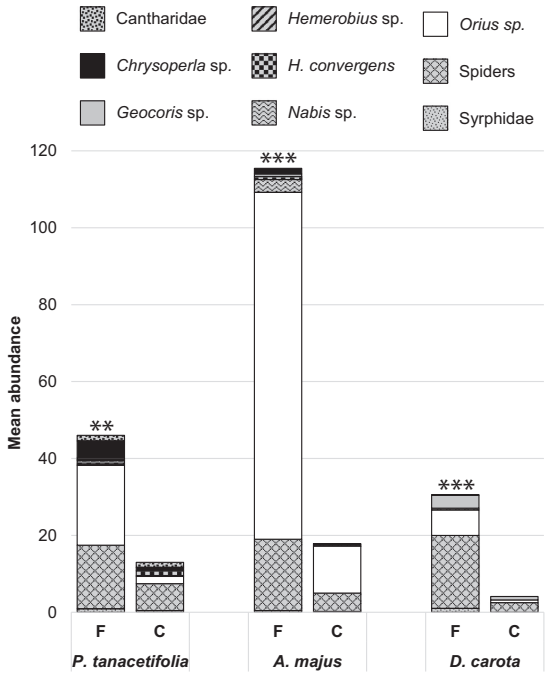

Fig. 1. Natural enemy densities on the ground covers in the flowering cover crop (F) and control plots (C). Samples were taken at peak bloom for each of the three species of flower. *Orius* sp. and spider densities were higher on all three species of flowering cover crop as compared with resident ground cover vegetation in the control plots, and there were more *Chrysoperla* sp. on *Phacelia tanacetifolia* and *Ammi majus* and more *Hippodamia convergens* and *Nabis* sp. on *A. majus*. $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

sp. densities, which were increased in plots with the flowering covers (Figs. 2, 3). Abundance of *Orius* sp. and total natural enemies was found to be increased at sites with more diverse landscapes as well, but decreased at sites with higher *E. elegantula* densities (Table 3). Natural enemy evenness demonstrated an inverse trend, with lower evenness in more diverse landscapes and higher evenness at sites with high *E. elegantula* densities.

In the late season, there were more hoverflies and spiders on vines in the plots with flowering cover crops, although specific spider families were more likely to be influenced by landscape diversity and/or increased *E. elegantula* densities (Table 3). Similar to early-season trends, abundance of *Orius* sp. and total natural enemies was elevated at sites with high levels of landscape diversity and high *E. elegantula* densities (Table 3). Again, natural enemy evenness exhibited inverse trends, with lower evenness at more diverse sites and higher evenness at sites with increased *E. elegantula* densities (Table 3).

Anagrus *and* Erythroneura elegantula *abundance and parasitism rate*

Early-season *Anagrus* spp. densities were positively influenced by flowering cover crops, increased landscape diversity, and *E. elegantula* abundance (Figs. 4, 5A, Table 1). Populations of early-season *E. elegantula* could not be explained by any of the variables examined (Fig. 5B, Table 1). Early-season parasitism of *E. elegantula*

Table 2. Influence of cover crop and landscape diversity on generalist predator densities on ground covers at peak bloom of each species of flowering cover crop.

	Phacelia tanacetifolia (n = 18)		*Ammi majus* (n = 18)		*Daucus carota* (n = 20)	
Generalist predator	Flowers	Landscape diversity	Flowers	Landscape diversity	Flowers	Landscape diversity
Cantharidae	0.13	0.38	...	...	...	...
Chrysoperla sp.	11.03***	0.00	9.75**	0.02	1.12	0.63
Geocoris sp.	2.26	0.00	3.86	1.07	1.96	0.88
Hemerobius sp.	1.13	0.69	...	...	...	...
Hippodamia convergens	0.50	0.61	5.32*	0.02	...	...
Nabis sp.	0.32	0.86	5.09*	0.04	2.98	0.84
Orius sp.	6.35**	0.14	12.92***	2.47	20.17***	0.45
Spiders	9.86**	0.81	15.15***	0.10	16.12***	1.43
Syrphidae	0.08	0.00	2.49	1.12	1.11	0.63
Evenness (J')	0.00	0.15	0.60	2.64	16.10***	2.08
Total abundance	8.72**	0.04	12.92***	2.77	15.55***	1.57

Note: Table shows χ^2 values from the linear mixed-effects models.
$^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

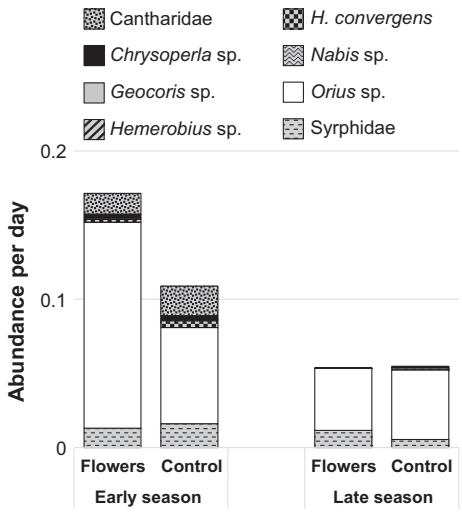

Fig. 2. Early- and late-season abundance of dominant natural enemy groups in the vine canopy in the flowering cover crop and control plots. Early-season densities of *Orius* sp. and late-season densities of Syrphidae were higher in the vine canopy in the presence of flowering cover crops.

eggs was associated with the interaction between *Anagrus* and *E. elegantula* densities, with higher parasitism rates observed at sites with a lower ratio of *E. elegantula* to *Anagrus* (Fig. 6, Table 1).

In the late season, *E. elegantula* populations were unaffected by the flowering cover crop (Fig. 5B), but strongly influenced by early-season *E. elegantula* density, followed by total petiole N content and early-season parasitism rate (Fig. 7, Table 1). Late-season densities of *Anagrus* spp. were strongly correlated with *E. elegantula* abundance (Table 1).

Crop vigor, yield, and quality

Flowering cover crops and landscape diversity did not have any influence on total petiole N content (flowers 0.7% ± 0.04%, control 0.7% ± 0.04% [cover: $\chi^2 = 0.15$, $P = 0.70$; landscape: $\chi^2 = 1.26$, $P = 0.26$; $n = 10$]), average cluster weight (kg per cluster: flowers 0.08 ± 0.03, control 0.07 ± 0.03 [cover: $\chi^2 = 0.45$, $P = 0.50$; landscape: $\chi^2 = 0.01$, $P = 0.94$; $n = 10$]), grape berry sugar levels (°Brix: flowers 24.5 ± 0.8, control 25.2 ± 0.6 [cover: $\chi^2 = 0.49$, $P = 0.49$; landscape: $\chi^2 = 2.72$, $P = 0.10$; $n = 10$]), or cane pruning weights (kg cane prunings per vine: flowers 0.5 ± 0.1, control 0.6 ± 0.1 [cover: $\chi^2 = 2.58$, $P = 0.11$; landscape: $\chi^2 = 2.61$, $P = 0.11$; $n = 10$]).

Landscape mediation of flowering cover crop effects

Differences in natural enemy abundance on ground covers in the plots with and without flowering cover crops did not change relative to landscape context (Table 4). In the crop canopy, a non-linear response was observed for *H. convergens* and *Orius* sp. densities, total natural enemy abundance and evenness, and *E. elegantula* parasitism rate (Fig. 8, Table 4). With the exception of *Orius* sp. and total natural enemy abundance, all of these variables exhibited the strongest response to the flowering cover crops in landscapes with intermediate diversity. In contrast, densities of *Orius* sp. and total natural enemy abundance had the most pronounced response to the flowering cover crops in landscapes with very low and very high diversity. When *Orius* sp. densities were removed from total natural enemy abundance, there was no longer an effect, indicating that the response was driven primarily by *Orius* sp.

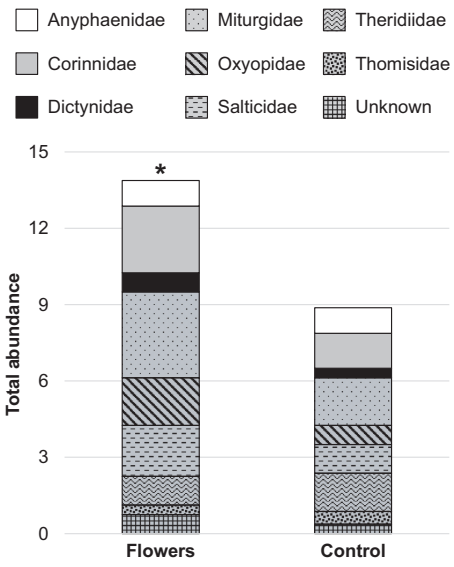

Fig. 3. Spider abundance in the vine canopy in the flowering cover crop and control plots. Total spider abundance was higher in the flowering cover crop plots, although no individual spider family was influenced by the flowers. $^*P \leq 0.05$.

Table 3. Influence of cover crop, landscape diversity, and pest density on generalist predator abundance and evenness (J') in the crop canopy during the early- and late-season periods.

	Early season			Late season		
Generalist predator	Flowers	Landscape diversity	*Erythroneura elegantula* density	Flowers	Landscape diversity	*E. elegantula* density
Cantharidae	0.76	0.83	0.06	. . .	. . .	. . .
Chrysoperla sp.	0.16	0.50	0.26	. . .	. . .	. . .
Geocoris sp.	. . .	. . .	. . .	. . .	. . .	. . .
Hemerobius sp.	. . .	. . .	. . .	. . .	. . .	. . .
Hippodamia convergens	2.20	3.75	0.06	3.26	1.83	1.87
Nabis sp.	. . .	. . .	. . .	. . .	. . .	. . .
Orius sp.	3.86*	6.82**	(6.56)*	0.51	14.06***	14.50***
Syrphidae	0.42	0.75	3.81	11.31***	0.10	2.04
Evenness (J')	2.51	(7.50)**	6.05*	3.47	(9.93)**	(6.75)**
(excl. *Orius* sp.)	0.01	0.10	0.94	. . .	. . .	. . .
Total abundance	2.33	4.9*	(4.14)*	0.03	13.24***	14.40***
(excl. *Orius* sp.)	1.57	0.38	0.18	2.89	0.29	0.08
Anyphaenidae				0.04	4.77*	1.66
Corinnidae				1.18	1.37	0.79
Dictynidae				0.66	0.21	1.29
Miturgidae				2.35	2.40	0.18
Oxyopidae				1.47	6.51**	4.65*
Salticidae				1.35	4.48*	2.84
Theridiidae				0.00	0.62	0.15
Thomisidae				0.07	0.21	0.11
Unknown				0.52	1.51	0.16
Spider evenness (J')				1.16	0.53	3.15
Spider abundance				4.28*	4.94*	1.65

Notes: Organisms in the top half of the table were collected with yellow sticky-traps ($n = 20$, except for analyses that exclude *Orius* sp. $n = 18$). Organisms in the bottom half of table were collected with beat-sheets ($n = 16$). Table shows χ^2 values from the mixed-effects models, and parentheses denote a negative relationship.

$^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

Discussion

Natural enemies on the flowering cover crops and in the vine canopy

The higher abundance and evenness of natural enemies on the ground covers in plots with flowering cover crops seen in this study are likely the result of increased availability of floral nectar, pollen, shelter, and/or alternate prey (Landis et al. 2000). Increased natural enemy populations on the flowering cover crops follow similar observations from previous vineyard cover crop trials (Altieri and Schmidt 1985, Costello and Daane 1998, 2003, Nicholls et al. 2000). However, natural enemy response to the flowering cover crops was much weaker in the vine canopy itself. This parallels the mixed results seen in earlier vineyard studies, some of which found that cover crops had no effect on the abundance of spiders (Daane and Costello 1998, Costello and Daane 2003) or *Anagrus* spp. (English-Loeb et al. 2003) in the vine canopy, while others have documented an increase in spiders (Nicholls et al. 2000, Hanna et al. 2003), *Chrysoperla* sp., Coccinellidae, *Geocoris* sp., *Nabis* sp., and *Orius* sp. (Nicholls et al. 2000) as well as predatory thrips and parasitoids in the families Eulophidae and Scelionidae and the genus Trichogramma (Danne et al. 2010).

Regardless of the flowering cover crops, total natural enemy abundance and evenness, and in particular densities of *Orius* sp. and spiders, in the crop canopy were all heavily influenced by changes in landscape diversity and *E. elegantula* densities. The increase in total natural enemy abundance in more diverse landscapes appears to have been driven solely by changes in *Orius* sp. densities (Table 3). Similarly, the relationship between natural enemy evenness, landscape diversity, and *E. elegantula* densities was no longer significant when *Orius* sp. densities were excluded

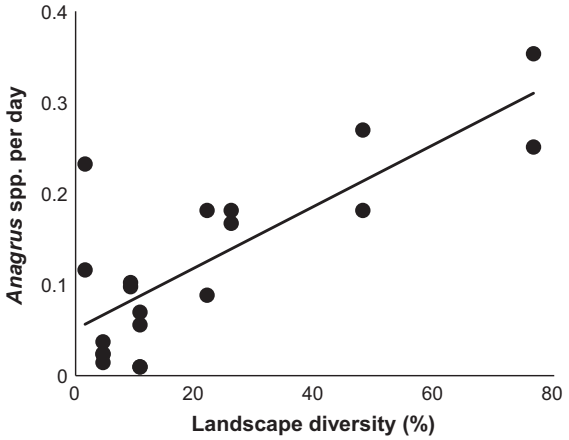

Fig. 4. Densities of *Anagrus* spp. per day in the vine canopy in the early season relative to the proportion of natural habitat within 0.5 km of the vineyard study site. Figure includes data from both the flowering cover crop and control plot at each site. Early-season *Anagrus* densities increased in more diverse landscapes (partial correlation = 0.82), regardless of the presence of flowering cover crops.

(Table 3). Essentially, the dominance of *Orius* sp. in the generalist predator community resulted in an inverse relationship with natural enemy evenness, with increased *Orius* sp. populations leading to a more uneven natural enemy community. Landscape influence on generalist predators (Bianchi et al. 2006, Chaplin-Kramer et al. 2011) and specifically *Orius* sp. (Prasifka et al. 2004, Werling et al. 2011, Veres et al. 2012) and spiders (Schmidt et al. 2005, Isaia et al. 2006, Hogg and Daane 2013) has been previously documented. The underlying mechanism driving these changes in abundance in the crop canopy at sites with increased landscape diversity is not entirely clear, but is likely related to increased availability of overwintering shelter, nectar, pollen, and/or alternate prey associated with the greater availability of natural habitats (Landis et al. 2000).

It is interesting that *Orius* sp. densities were generally increased in the crop canopy at sites in more diverse landscapes (Table 3), but they were not similarly elevated on all ground covers (i.e., both flowers and weeds) at these same sites (Table 2), even though data from the crop canopy indicate that these high-diversity landscapes appear to support greater overall populations of *Orius* sp. This is likely because in diverse landscapes with high densities of *Orius* sp. the crop canopy in treatment and control plots presents an equally suitable habitat and therefore increased abundance is observed regardless of ground cover type. Alternately, on the actual ground covers, flowering cover crops are disproportionately attractive relative to resident weedy vegetation, which consistently did not attract any natural enemies, including *Orius* sp., regardless of landscape diversity. Therefore when evaluating the response of *Orius* sp. on all ground covers relative to changes in landscape diversity, a response similar to what was seen in the crop canopy was not observed on the ground covers.

Higher *E. elegantula* densities at sites with low early-season *Orius* sp. densities could be a sign of natural enemy release and, alternately, high late-season *Orius* sp. and spider densities at sites

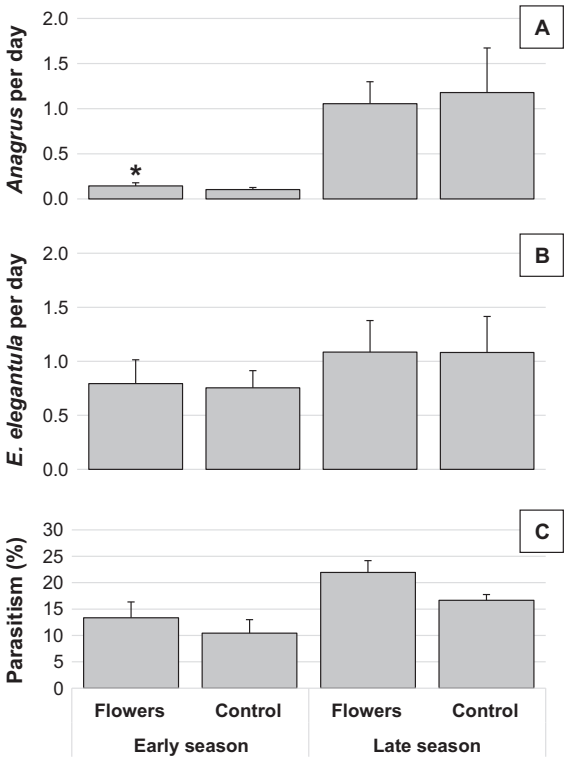

Fig. 5. Abundance of *Anagrus* spp. (A), *Erythroneura elegantula* (B), and *E. elegantula* parasitism rates (C) in the vine canopy from flowering cover crop and control plots in the early and late season. Early-season *Anagrus* densities were higher in the flowering cover crop plots, while *E. elegantula* densities and parasitism rate were unaffected ($^*P < 0.05$).

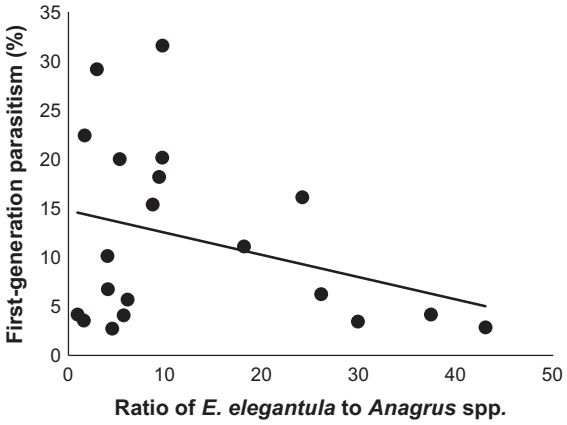

Fig. 6. Parasitism rate of first-generation *Erythroneura elegantula* relative to the early-season ratio of *E. elegantula* to *Anagrus* spp. abundance in the vine canopy. Early-season parasitism rate was determined by the ratio of *E. elegantula* to *Anagrus* spp.

with large *E. elegantula* populations could be a numeric response to increased prey availability (Kidd and Jervis 2005). Whether or not these early- and late-season differences in *E. elegantula*, *Orius* sp., and spider densities had any effect on predation pressure is unclear though, since no evaluation was included in this study. While the effect of *Orius* sp. and spider predation on *E. elegantula* is here unknown, it is likely minor relative to the impact of *Anagrus*, especially given the overall low predator population in the canopy (Figs. 2, 3), previous evidence that it would take a substantial increase in predator abundance to significantly reduce vineyard leafhopper populations (Hanna et al. 2003) and the fact that *Orius* sp. is primarily known as a predator of smaller insects such as thrips and mites.

Anagrus *and* Erythroneura elegantula *densities—early season*

Landscape diversity had the strongest influence on early-season *Anagrus* densities. Higher abundance of *Anagrus* spp. in more diverse landscapes has been previously documented (Murphy et al. 1996, Wilson et al. 2015*a*) and is very likely due to the close proximity of overwintering habitat (Doutt and Nakata 1973, Williams and Martinson 2000). Early-season *Anagrus* response to the flowering cover crops is likely the result of increased floral nectar, which is a key limiting factor for these minute parasitoids (English-Loeb et al. 2003, Segoli and Rosenheim 2013). Correlation between *Anagrus* and *E. elegantula* abundance is a known density-dependent response that has been observed in other vineyard studies (Murphy et al. 1998, Nicholls et al. 2000, Wilson et al. 2015*a*).

Early-season density of *E. elegantula* was not explained by any of the factors included in this analysis. Previous work has shown that early-season leafhopper populations are strongly determined by late-season abundance in the previous year (Wilson et al. 2015*a*), although here it was not possible to evaluate this effect due to the limited number of repeat sites in the second year of this study.

Parasitism rate—early season

Even with the slight increase in *Anagrus* densities in the flowering cover crop plots, parasitism rates were unaffected by the flowers, which matches findings from previous studies (Daane

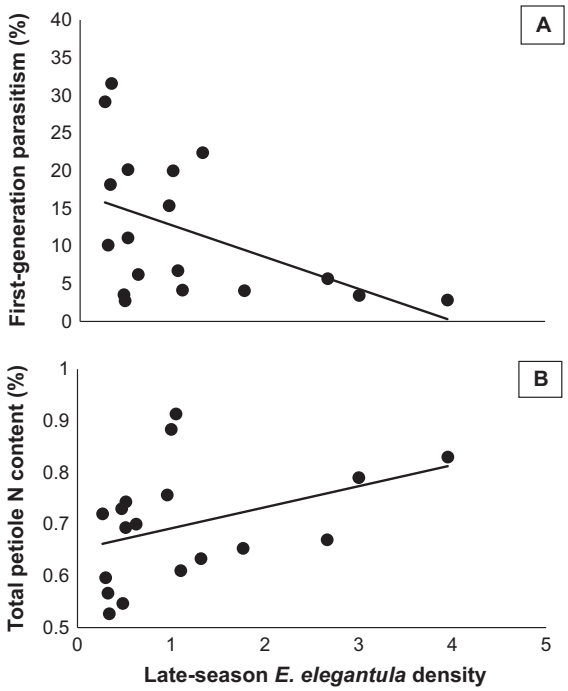

Fig. 7. Late-season *Erythroneura elegantula* densities were increased at sites with low early-season parasitism rates (A, partial correlation = −0.56) as well as at sites with high vine vigor (B, partial correlation = 0.67), regardless of flowering cover crops or landscape diversity.

Table 4. Landscape mediation of flowering cover crop effects.

Response variable	Flowering cover crop			Vine canopy		
	Linear	Polynomial	*n*	Linear	Polynomial	*n*
Anagrus spp.	. . .	. . .	. . .	0.15	0.05	20
Erythroneura elegantula	. . .	. . .	. . .	0.06	0.09	20
Parasitism rate (early season)	. . .	. . .	. . .	4.65*	6.33**	10
Cantharidae	0.00	0.06	28	0.02	0.04	20
Chrysoperla sp.	0.60	0.77	28	0.66	0.54	20
Geocoris sp.	0.10	0.27	28	0.31	0.97	20
Hemerobius sp.	0.72	0.43	28	0.21	0.19	20
Hippodamia convergens	1.32	0.72	28	2.64	4.94*	20
Nabis sp.	3.27	2.76	28	. . .	. . .	–
Orius sp.	0.51	2.65	28	(4.14)*	(5.71)*	20
Spiders	0.54	0.34	28	0.05	0.06	8
Syrphidae	3.68	2.48	28	0.15	0.14	20
Evenness (J')	0.66	0.05	15	4.50*	4.81*	18
Evenness (J') (excl. *Orius* sp.)	. . .	. . .	. . .	0.97	1.43	9
Total abundance	0.38	2.21	28	3.14	(4.30)*	20
Total abundance (excl. *Orius* sp.)	. . .	. . .	. . .	0.01	0.00	20

Notes: For each response variable, the difference between the treatment and control plot at each site was evaluated with a model that included a linear and non-linear term (i.e., polynomial) for the main effect "landscape diversity." Table shows χ^2 values from this analysis, and parentheses denote a negative effect.
$^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

and Costello 1998, Nicholls et al. 2000, English-Loeb et al. 2003). Increased densities of *Anagrus* in more diverse landscapes only translated into higher parasitism rates when there were adequate densities of *E. elegantula* to attack; therefore, the ratio of *E. elegantula* to *Anagrus* was the strongest determinant of early-season parasitism rates (Fig. 6), which has been previously documented (Wilson et al. 2015*a*).

Anagrus *and* Erythroneura elegantula *densities—late season*

Late-season abundance of *Anagrus* was strongly driven by a density-dependent relationship with *E. elegantula*, which has been frequently reported (Murphy et al. 1998, Nicholls et al. 2000, Williams and Martinson 2000, Wilson et al. 2015*a*, *b*). While previous studies have recorded lower densities of *Erythroneura* leafhoppers in the presence of cover crops (Daane and Costello 1998, Nicholls et al. 2000, Costello and Daane 2003), others have not (English-Loeb et al. 2003, Hanna et al. 2003). In those cases where leafhopper densities were reduced in the presence of a cover crop, there was no observable change in parasitism rate and so it was concluded that reduced densities were the result of either increased predation (Nicholls et al. 2000) or reduced vine vigor due to competition for water or nutrients from the cover crop (Costello and Daane 2003). Here, the flowering cover crop had no impact on late-season leafhopper densities, nor did it impact crop vigor, yield, or quality. Rather, late-season *E. elegantula* densities were lower at sites with generally reduced vigor, regardless of flowering cover crop or landscape diversity, which has been well documented elsewhere (Daane and Costello 1998, Daane and Williams 2003, Wilson et al. 2015*a*). Late-season *E. elegantula* populations were also reduced at sites with a high early-season parasitism rate, which is considered a key condition for late-season leafhopper control (Doutt and Nakata 1973, Daane et al. 2013) and demonstrated in other studies (Murphy et al. 1998, Wilson et al. 2015*a*).

Cover crop and landscape interaction

Natural enemy abundance and impact in the crop canopy exhibited a non-linear response to the presence of flowering cover crops across different landscapes, which suggests that the effect of this local diversification practice can in some cases be mediated by landscape diversity. Here, the greatest increase in *H. convergens* abundance and *E. elegantula* parasitism rate was observed in plots with flowering cover crops at sites with intermediate levels of landscape diversity (Fig. 8A, Table 4).

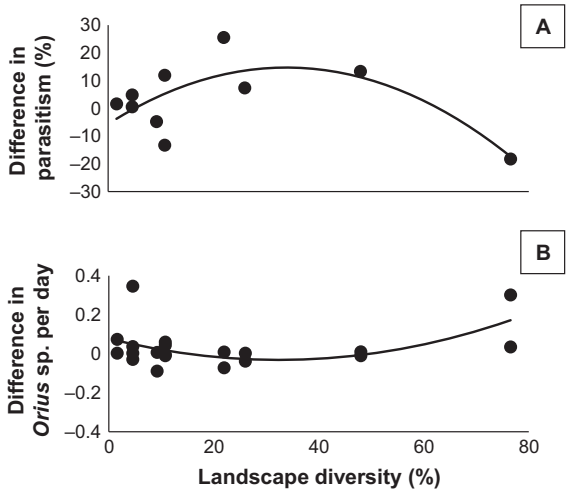

Fig. 8. The presence of the flowering cover crop had the strongest effect on parasitism rate in intermediate landscapes (A), while *Orius* sp. densities in the vine canopy followed an inverse trend (B). For each variable, *y*-axis values are the difference between the flowering cover crop plot and control plot at each site. Higher values indicate a relatively higher response in the flowering cover crop plot relative to the control.

This follows the "intermediate landscape complexity hypothesis," which suggests that natural enemy response to local diversification will be strongest in landscapes with intermediate levels of diversity because high-diversity landscapes already contain adequate resources for natural enemies, while low-diversity landscapes are unable to support sufficient meta-populations (Tscharntke et al. 2012).

Abundance of *Orius* sp. also exhibited a non-linear response to the flowering cover crops, but surprisingly it was an inverse trend (Fig. 8B), with greater densities observed in flowering cover crop plots at sites with either very low or very high landscape diversity. Total natural enemy abundance and evenness also exhibited non-linear trends, but it appears to be entirely driven by *Orius* sp. densities. When *Orius* sp. was excluded from total abundance and evenness, there was no longer a relationship for either response variable (Table 4). No previous studies have evaluated landscape mediation of *Orius* spp. response to local habitat diversification. The response observed here represents a unique, inverse example of the "intermediate landscape complexity hypothesis" that has not been documented in any other study. As a polyphagous organism that does not necessarily have an obligatory, functional tie to natural habitats, *Orius* spp. may exhibit unique responses to changes in local and landscape diversity, and to the provision of floral resources in particular. While *Orius* spp. has been shown to respond to increased landscape diversity (Prasifka et al. 2004), the trend is not always consistent (Werling et al. 2011, Wilson et al. 2015*a*) and in some cases *Orius* spp. actually appear to be more strongly associated with agricultural habitats (Veres et al. 2012), which may be due to the increased availability of preferred prey items, such as thrips and mites. Previous studies have demonstrated that *Orius* sp. longevity and fecundity are enhanced by a mixed diet that includes pollen and thrips or mites (Salas-Aguilar and Ehler 1977, Kiman and Yeargan 1985) and in vineyards, both thrips (*Frankliniella occidentalis* (Pergande)) and mites (*Tetranychus pacificus* McGregor, *Eotetranychus willamettei* (McGregor)) are commonly found in high densities (Phillips et al. 2013, Zalom et al. 2013). Therefore, it may be that *Orius* sp. makes use of both natural and agricultural habitats, benefitting from pollen in natural habitats and insect prey like *F. occidentalis*, *T. pacificus*, and *E. willamettei* in vineyards. As such, intermediate landscapes that contain a more equal mix of agricultural and natural habitats may actually provide complimentary resources for *Orius* sp., which are then less likely to respond to the presence of flowering cover crops due to the availability of pollen in natural habitats and alternate prey in agricultural habitats. In contrast, flowering cover crops attract *Orius* sp. in simplified landscapes because they provide pollen, which is likely limited due to a lack of natural habitat, and in highly diverse landscapes the flowers provide alternate prey, which are possibly limited due to decreased area of vineyard. The result is increased *Orius* sp. aggregation in plots with flowering cover crops in simplified and highly diverse landscapes, but not in intermediate landscapes. Further evaluation would be required to verify this, as densities of alternate prey for *Orius* sp. were not recorded in this study.

While enhanced efficacy of local diversification in intermediate-diversity landscapes has been broadly documented in a number of studies

(Batáry et al. 2011, Tuck et al. 2014), outcomes are not always consistent and vary between species (Clough et al. 2005, Roschewitz et al. 2005, Kleijn and Van Langevelde 2006, Haenke et al. 2009, Woltz et al. 2012, Midega et al. 2014, Rusch et al. 2014). The few studies that have specifically examined the interaction between floral resource provisioning and landscape diversity have produced similarly mixed results. For example, strips of buckwheat (*Fagopyrum esculentum* L.) sown adjacent to fields of kale (*Brassica oleraceae* L.) did lead to enhanced parasitism in intermediate landscapes (Jonsson et al. 2015), yet a similar experiments in soy bean (*Glycine max* L.) did not lead to any specific local × landscape interactions (Woltz et al. 2012). In vineyards, previous studies have shown that changes in landscape and local diversity can lead to changes in the composition of spider communities (Isaia et al. 2006, Hogg et al. 2010, Hogg and Daane 2013), although none have evaluated the interaction between diversification at these two spatial scales. Ultimately, the degree to which landscape diversity mediates the influence of flowering cover crops on a given species is contingent upon a variety of factors, including habitat and nutritional requirements, dispersal capacity, and meta-population stability (Tscharntke et al. 2005).

Conclusion

The ability of flowering cover crops to attract large populations of natural enemies did not appear to translate into higher abundance in the vine canopy itself, much less lead to any increase in biological control of *E. elegantula* or, most importantly, a reduction in late-season populations of this pest. While the flowering cover crop did not affect crop vigor, yield, or quality, leafhopper densities were generally reduced at sites with lower vigor. Regardless of flowering cover crops, vineyards situated in more diverse landscapes tended to have higher densities of *Anagrus* in the early season, which resulted in a lower ratio of *E. elegantula* to *Anagrus* that subsequently led to increased parasitism and decreased late-season *E. elegantula* populations. In some instances, landscape diversity did appear to moderate the effect of flowering cover crops on natural enemy abundance and pest parasitism rates, although ultimately these changes did not have any influence on late-season leafhopper populations. While habitat diversity is critical to the management of ecosystem services in agriculture, the differential effects of local and landscape diversity seen here highlight the importance of spatial scale in the design of ecologically based pest management strategies. Furthermore, this study demonstrates how biological control can be influenced by multiple, complementary variables, such as habitat diversity and crop vigor.

Acknowledgments

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