Influence of Vineyard Vegetational Borders on Western Grape Leafhopper (*Erythroneura elegantula* Osborn), its Egg Parasitoids (*Anagrus* spp.) and Generalist Insect Predators

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Studies have shown that vegetational diversity in or around cropping systems can enhance natural enemy abundance, although the impact on herbivores is less certain. We studied the influence of vineyard vegetational borders on density of the western grape leafhopper, *Erythroneura elegantula*, its major parasitoids, *Anagrus* spp., and two generalist predators, *Orius* spp. and *Leptothrips mali*. Two study vineyards had planted, perennial flowering hedgerows, one bordered a natural riparian zone, and one had a sparse border of native trees. From April to September 2007, we counted leafhopper nymphs and adults of *Anagrus* spp., *Orius* spp. and *L. mali* within 10 m of the border, and at additional 20 m intervals up to 90 m. At two sites with a diverse border, leafhopper density was stable nearest the border; at other distances leafhopper density decreased between the first and second generations. This effect was not seen at the sparse border site. *Anagrus* spp. density was enhanced at one site with a diverse border, but only late season. There was no border effect on the generalist insect predators, by site or early vs. late season. Regression analysis showed a positive relationship between leafhopper and *Anagrus* spp. density, suggesting that the parasitoids were responding to higher leafhopper density. We conclude that, depending on the nature of the border vegetation, there can be an effect on leafhopper nymphal density, but in this study there is no evidence that it was due to natural enemies.

INTRODUCTION

Vegetational diversity and its effects on insect pests and their natural enemies have been studied in a wide variety of cropping systems (see reviews by Andow, 1991; Landis *et al.*, 2000; Letourneau *et al.*, 2011). Ratnadass *et al.* (2012) identify eight pathways in which vegetational diversity can impact agricultural pests, which include top down effects on arthropods through natural enemy conservation. The concept that non-crop plantings can influence arthropod natural enemies, known as the enemies hypothesis (Root, 1973; Russell, 1989), says that the alternative vegetation can provide alternate food sources (Wäckers *et al.*, 2007), or shelter and overwintering sites (Landis *et al.*, 2000). Theorists have suggested that agroecosystems should mimic more diverse natural ecosystems, which will improve the stability of insect communities at higher trophic levels (Haddad *et al.*, 2011). Although most reviews on vegetational diversity in agriculture (Russell, 1989; Andow, 1991; Landis *et al.*, 2000; Wäckers *et al.*, 2007; Jonsson *et al.*, 2008; Letourneau *et al.*, 2011; Ratnadass *et al.*, 2012) have concluded that increased diversity is associated with higher natural enemy populations, interpretations vary with respect to herbivore injury, with some attesting a trend towards lower herbivore injury (Letourneau *et al.*, 2011), and others indicating that there is little evidence for this (Jonsson *et al.*, 2008). Part of the reason for this is, no doubt, the wide variety of diversification schemes.

Perennial cropping systems can be diversified by managing non-crop vegetation, within or adjacent to the cultivated area, or by preserving adjacent native vegetation. Within field vegetation consists of planted cover crops or naturalized (i.e. non-native, but established) vegetation; this has the advantage of having a more uniform distribution of any beneficial effect throughout the field, yet drawbacks include possible competition with the commercial crop or interference with crop management. The alternative is the planting or preservation of field margin vegetation, i.e.

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perennial hedgerows or native vegetation areas which border the cropping system, to provide stable natural enemy habitat. However, in most systems it is not known how far any effect will carry from the border into the cultivated area. When effects have been found, they tended to have a limit from the border vegetation into the main crop, estimated by previous studies at 40 m (Thompson & Hoffman, 2013) or 60 m (Griffiths *et al.,* 2008).

In commercial grape vineyards, several studies have been conducted in California on the role of border vegetation on the western grape leafhopper (WGLH), *Erythroneura elegantula* Osborn (Hemiptera: Cicadellidae) and its major parasitoids, *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *Anagrus daanei* Triapitsyn (Hymenoptera: Mymaridae). This community is an excellent one for testing the influence of vegetational borders, not only because the non-crop vegetation may provide food resources for the natural enemies, but WGLH and *Anagrus* spp. migrate in the autumn and overwinter on non-grape vegetation (Daane *et al.*, 2013), and therefore nearby alternative vegetation might play a role in providing shelter and overwintering sites. WGLH feeds in the adult and nymphal stages by sucking out the contents of cells in the mesophyll region, which can lead to a reduction in photosynthetic activity. Leafhopper eggs are laid just under the leaf epidermis, and are parasitized by *Anagrus* spp. WGLH overwinters as an adult and feeds on weedy and perennial evergreen vegetation during the winter; *Anagrus* spp. overwinter by ovipositing into the eggs of non *Erythroneura* leafhopper species. Corbett and Rosenheim (1996) studied the effect of a prune tree border as an overwintering refuge for *Anagrus* spp., finding that the refuge contributed significantly to immigrating *Anagrus* spp., and also created a windstream that generated a pattern of *Anagrus* spp. abundance immediately downwind of the refuge. Nicholls *et al.* (2001) and Wilson *et al.* (2015a) studied the effects of permanent border vegetation (flowering vegetational corridors or native riparian areas) on WGLH and *Anagrus* spp., each finding that the border vegetation contributed to lower leafhopper abundance in the most adjacent plot. However, a positive effect on *Anagrus* spp. density was not found by Nicholls *et al.* (2001), and was found by Wilson *et al.* (2015a) only in the early season. Wilson *et al.* (2015b) found an early season enhancement of *Anagrus* spp. when analyzing the effects of landscape diversity. Gaigher *et al.* (2015) studied the influence of natural scrubland of South Africa on hymenopteran parasitoid abundance and diversity in an adjacent commercial vineyard, finding that the parasitoid assemblage differed considerably between the natural area and the vineyard. In Israel, Shapira *et al.* (2018) found that a vineyard adjacent to a natural area supported high densities of natural enemies during the growing season, and high numbers of *Anagyrus* sp. nr. *pseudococci* (the main parasitoid of the vine mealybug, *Planococcus ficus*) in winter.

Results on studies of the effects of vegetational diversity on generalist arthropod predators in vineyards have been mixed. Judt *et al.* (2019) found that landscape diversity had a positive influence on spider abundance, but not other generalist predators, in Andalusian vineyards. Thomson and Hoffman (2009, 2013) found a trend of higher density of a number of generalist predators on vines closest to a woody vegetation border, including coccinellids, staphylinids and predatory thrips, although Thomson *et al.* (2010) did not find a consistent effect of landscape diversity on vineyard generalist predators. Nichols *et al.* (2001) found a trend towards higher densities of generalist predator groups, including coccinellids, nabids, chrysopids and syrphids, on vines closest to forested borders or flowering corridors. Wilson *et al.* (2015b) did not find a significant correlation between landscape diversity and genera such as *Orius* and *Chrysoperla*, although in a separate study they did find a positive effect of flowering cover crops on these groups, and found that the only predatory group positively affected was *Orius* spp. (Wilson *et al.*, 2017).

We studied four commercial vineyard sites in northern California and analyzed the influence of vegetational borders on density of WGLH, *Anagrus* spp. and generalist predators. Our field sites spanned a range of vegetational diversity: two had planted, highly diverse, perennial flowering hedgerows, one had a diverse natural riparian zone as a border, and one was bordered by a sparse row of two species of native trees. Agroecosystem theory states that vegetative zones with the most diversity, and providing floral resources, would be the most attractive to and harbor more natural enemies (Bianchi & Wäckers, 2008). We also recorded generalist arthropod predators, most of which were not abundant enough to be analyzed statistically; however, *Leptothrips mali* (Fitch) (Thysanoptera: Phlaeothripidae) and *Orius* spp. (Hemiptera: Anthocoridae), were found in sufficient density and are presented here. Our objectives were to evaluate densities of these insects in relation to proximity to vegetational borders, as well as seasonality.

MATERIALS AND METHODS

Field sites

Details of the field sites are summarized in Table 1, and consisted of three sites within the Russian River Valley near Hopland, Mendocino County: Bonterra (McNab Ranch), Fetzer (Sundial Ranch) and Milovina, and one site near Glen Ellen, Sonoma County: Benziger.

Vegetation represented at the study sites is listed in Table 2; the borders at Bonterra and Benziger consisted of a hedgerow or shelterbelt of a diversity of primarily exotic perennials, designed so that at least one component of the planting was in flower over the course of the grape growing season (1 April to 30 October). At Bonterra the vegetation was established as a linear hedgerow along the western border of the vineyard, whereas at Benziger a shelterbelt was planted in the middle of the vineyard in a circular pattern. The Fetzer vineyard was located along the Russian River and the border vegetation consisted primarily of native riparian perennials (Table 2).

The Milovina site was the least diverse of all, and the margin consisted of a southern border of five established native oak trees (valley oak, *Quercus lobata*) and one native poplar (Fremont poplar, *Populus fremontii*), with all of the understory vegetation removed. No insecticides were applied at any site; the only pesticides applied on the vines were fungicides for control of powdery mildew (*Erysiphe necator*) (Table 1).

TABLE 1
Vineyard study site locations, grape variety and rootstock, type of vegetational border, distance to vineyard edge and summary of fungicide use (for control of *Erysiphe necator*).

Vineyard	Location	Variety/rootstock	Vegetational border/distance to vineyard edge	Pesticides
Bonterra	Russian River Valley, Mendocino County	Merlot/5C	Mostly exotic perennial hedgerow on western border/three meters	Sulfur and copper
Fetzer	Russian River Valley, Mendocino County	Chardonnay/AxR1	Mostly native riparian zone on western border/ten meters	Horticultural oil Sulfur
Benziger	Glen Ellen, Sonoma County	Sauvignon blanc	30 m diameter shelterbelt, mostly exotic perennial planting/ten meters	*Bacillus subtilis* (Serenade®) Sulfur
Milovina	Russian River Valley, Mendocino County	Chardonnay	Six mature native trees (five valley oaks, *Q. lobata,* and one Fremont cottonwood, *P. fremontii*, on the southern border /ten meters	Myclobutanil (Rally®) Sulfur

Single row plots were established at each site along a gradient from the border vegetation. The distance from the border vegetation to the vineyard edge (i.e., the roadway used for vehicle and equipment transport) was approximately 10 m at Fetzer, Milovina and Benziger, and 3 m at Bonterra (Table 1), and four adjacent plots were sampled at 20 m increments (i.e., 30 m, 50 m, 70 m and 90 m from the border vegetation).

Data collection

At each site, we counted leafhopper nymphs on 30 leaves per plot every two weeks, from April to September 2007. To collect *Anagrus* spp. and generalist predators, we placed one yellow sticky card (178 mm x 101 mm, Seabright, Emeryville, CA, USA) within the vine canopy of the 10 m plot (i.e. the border plot), and in the 30 m, 50 m, 70 m and 90 m plots. We changed cards every two weeks and recorded adults per card.

Data analysis

Leafhopper nymphs per leaf, *Anagrus* spp. per card and pooled *Orius* spp./*L. mali* per card were log10 transformed and analyzed by analysis of variance (ANOVA), using a mixed linear model, using site, distance and the interaction between site and distance as fixed effects and date as a random effect (PROC MIXED, SAS Institute 2012), and using least squared means with the Tukey adjustment for mean separation. *Orius* spp. and *L. mali* data were pooled for illustrative purposes, as the results did not differ from separate analyses. *Anagrus* spp. and *Orius* spp./*L. mali* were analyzed by early and late season time periods, which corresponded to analysis of the first and second leafhopper generations, which were estimated by site and defined by date range in Table 3. The ANOVA was considered statistically significant at $p<0.05$.

Mean *Anagrus* spp., *Orius* spp. and *L. mali* per card (log10) were regressed against mean leafhopper nymphal density per leaf (log10) on each sampling date for the early to mid season and mid to late season time period (corresponding to the first and second leafhopper generations), pooling the data across all sites (PROG REG, SAS Institute 2012). *Orius* spp. and *L. mali* data were not pooled for the regressions.

RESULTS

Leafhopper density

Mean first generation leafhopper density (across all dates for each distance) was highest at Bonterra (3.0 nymphs/leaf) and lowest at Fetzer (0.38 nymphs/leaf), with no nymphs counted at Benziger (Fig. 1), whereas mean second generation leafhopper density was highest at Milovina (1.26 nymphs/leaf) and lowest at Benziger (0.06 nymphs/leaf) (Fig. 2).

At three of the four sites, leafhopper nymphal density decreased from first to second generations, independent of *Anagrus* spp. density. Except for Benziger, where few leafhoppers were counted, second generation nymphal density was 63.5, 75.5, and 26% lower at Fetzer, Bonterra, Milovina, respectively, compared to the first generation ($p<0.001$). For first generation leafhoppers, there was significant interaction between site and distance ($F = 2.87$, df = 8, 2081, $p = 0.004$), in that at the Bonterra site nymphal density in the border plot was an average of 43.8% lower than in the 70 m or 90 m plots ($p<0.001$), but there was no significant distance effect at the other sites (Fig. 1). There was also significant interaction between site and distance for second generation nymphal density ($F = 15.86$, df = 8, 2230, $p<0.001$), again the effect being at Bonterra, but the trend reversed from the first generation: nymphal density in the border plot was significantly higher than all other plots, by 1.17, 1.81, 2.88 and 4.43 fold, compared to the 30 m, 50 m, 70 m and 90 m plots, respectively ($p<0.001$, Fig. 2). This resulted because leafhopper density in the border plot remained the same between generations ($p = 0.815$), whereas density declined at all other distances from first to second generation ($p<0.001$) (Figs. 1 and 2). In addition, second generation leafhopper density in the 30 m plot was 78.5% higher than at 70 m ($p = 0.039$) and 1.47 fold higher than at 90 m ($p<0.001$) (Fig. 2). There were no significant distance effects in second generation leafhopper nymphal density at the other sites (Fig. 2).

TABLE 2
List of plant species and associated families in the vegetative borders at the vineyard study sites.

Site	Family	Species	
Bonterra	Asteraceae	*Foeniculum vulgare*	*Gaillardia* sp.
		Echinacea purpurea	*Chrysanthemum parthenium*
		Achillea millefolium	*Coreopsis verticillata*
		Artemisia sp.	*Aster frikartii*
	Buddlejaceae	*Buddleia davidii*	
	Euphorbiaceae	*Euphorbia lathyris*	
	Lamiaceae	*Rosmarinus officinalis*	*Nepeta x fassenii*
		Origanum vulgare	*Lavendula* spp.
	Linaceae	*Linum perenne*	
	Lythraceae	*Punica granatum*	
	Moraceae	*Ficus carica*	
	Myrtaceae	*Feijoa sellowiana*	
	Onagraceae	*Gaura lindheimeri*	
	Poaceae	*Cortaderia selloana*	*Stipa arundinacea*
		Digitaria sanguinalis	
	Rosaceae	*Prunus persica*	*Rosa* sp.
		Mespilus germanica	
	Salicaceae	*Salix exigua*	
	Verbenaceae	*Verbena peruviana*	
Fetzer	Anacardiaceae	*Rhus diversiloba*	
	Apiaceae	*Conium maculatum*	
	Caprifoliaceae	*Dipsacus sylvestris*	
	Caprifoliaceae	*Symphoricarpos albus*	
	Fagaceae	*Quercus lobata*	
	Juglandaceae	*Juglans hindsii*	
	Oleaceae	*Fraxinus latifolia*	
	Rosaceae	*Rubus procerus*	*Rosa multiflora*
	Salicaceae	*Salix exigua*	*Populus fremontii*
	Sapindaceae	*Acer negundo*	
Benziger	Asparagaceae	*Yucca gloriosa*	
	Asteraceae	*Achillea tomentosa*	*Rudbeckia hirta*
		Ratibida columnifera	*Echinacea purpurea*
	Lamiaceae	*Hyssopus officinalis*	*Nepeta x faassenii*
		Salvia spp.	*Perovskia atriplicifolia*
	Onagraceae	*Epilobium canum*	
	Plantaginaceae	*Penstemon* spp.	
	Xanthorrhoeaceae	*Kniphofia uvaria*	
Milovina	Fagaceae	*Quercus lobata*	
	Salicaceae	*Populus fremontii*	

Anagrus spp. density

Early season *Anagrus* spp. density was highest at Bonterra (34.3 *Anagrus* spp./card) and lowest at Benziger (2.95 *Anagrus* spp./card) (Fig. 3), whereas late season density was highest at Milovina (296 *Anagrus* spp./card) and lowest at Benziger (8.6 *Anagrus* spp./card) (Fig. 4).

For early season *Anagrus* spp. there was no overall distance effect, but there was interaction between site and distance (F = 2.30, df = 12, 57, p = 0.018). Only at Bonterra was the distance effect significant, with density in the border plot 54.5% lower than in the 70 m plot (p = 0.022, Fig. 3). For late season *Anagrus* spp. there was an overall distance effect (F = 3.67, df = 4, 76, p = 0.008), with the border plot 17.2% higher than the 30 m plot (p = 0.01) and 32.8% higher than the 50 m plot (p = 0.018), and no interaction between site and distance, although the effect was clearly driven by the Fetzer, Bonterra and Benziger sites (Fig. 4).

Leptothrips mali and *Orius* spp. density

Early season density of the generalist predators *L. mali* and *Orius* spp. was significantly higher at the Fetzer site than at the other sites (2.8 times higher than at Bonterra or Milovina, and 19.6 times higher than Benziger) (p<0.01, Fig. 5), but there was no effect of distance and no interaction between site and distance. Late season generalist predator density was significantly higher at the Milovina site than the other sites (3.8 times higher than at Bonterra and 17.6 times higher than at Fetzer or Benziger) (p<0.001, Fig. 6). In addition, late season predator density at Bonterra was 4.6 times higher than at Fetzer or Benziger (p<0.001, Fig. 6). There was no significant effect of distance on late season predatory density, nor was there interaction between distance and site.

Regression analyses

Regression analysis showed a positive relationship between *Anagrus* spp. density and nymphal density for the first leafhopper generation (y = 0.44 + 1.31x, p<0.001), as well as the second leafhopper generation (y = 1.30 + 2.87x, p<0.001) (Fig. 7). Leafhopper density explained 67% of *Anagrus* spp. density in the first leafhopper generation and 73% in the second generation (Fig. 7).

There was a negative relationship between *Orius* spp. density and leafhopper nymphal density for the first leafhopper generation (y = 1.12 – 1.15x, p=0.003), with 47%

TABLE 3

Sampling date ranges (2007) for analysis of early and late season *Anagrus* spp. density, corresponding to the first and second generations of leafhoppers.

Site	Early season/1st leafhopper generation	Late season/2nd leafhopper generation
Fetzer	30 May-6 July	20 July-14 Sept
Bonterra	21 May-29 June	13 July-7 Sept
Milovina	30 May-9 July	30 July-20 Sept
Benziger	20 April-14 June	29 June-22 Sept

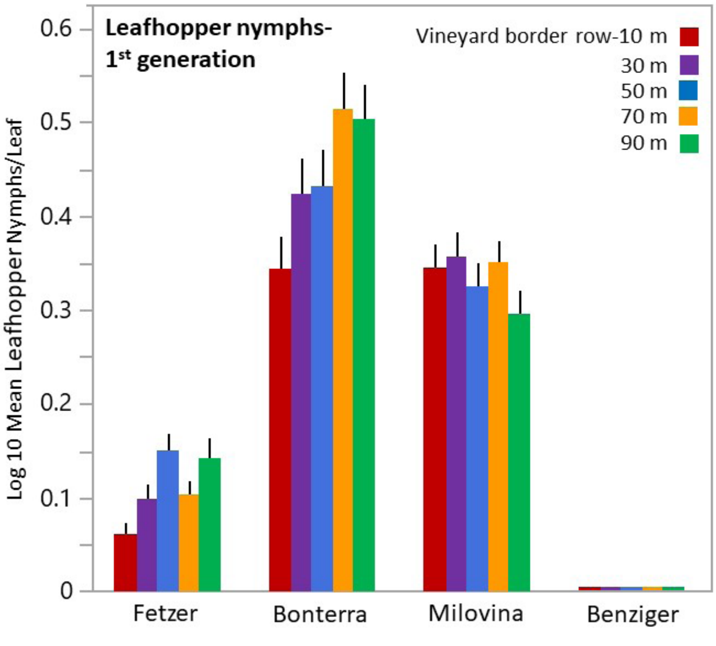

FIGURE 1

Mean first generation leafhopper nymphal density (log10 mean ± standard error of the mean) by site and distance. At Bonterra, leafhopper density in the border plot averaged 43.8% lower than the 70 m or 90 m plots (p<0.001).

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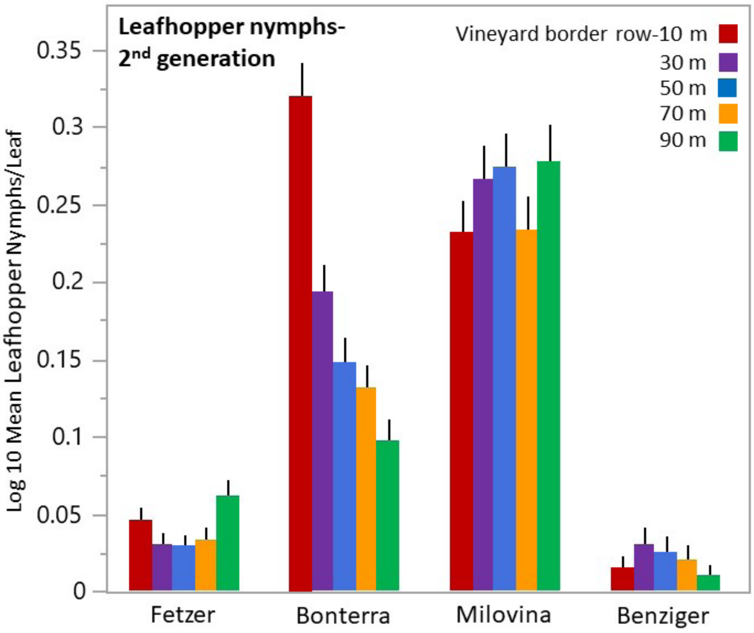

FIGURE 2
Mean second generation leafhopper nymphal density (log10 mean ± standard error of the mean) by site and distance. At Bonterra, leafhopper density in the border plot was 1.17, 1.81, 2.88 and 4.43 fold higher, compared to the 30 m, 50 m, 70 m and 90 m plots, respectively (p<0.001).

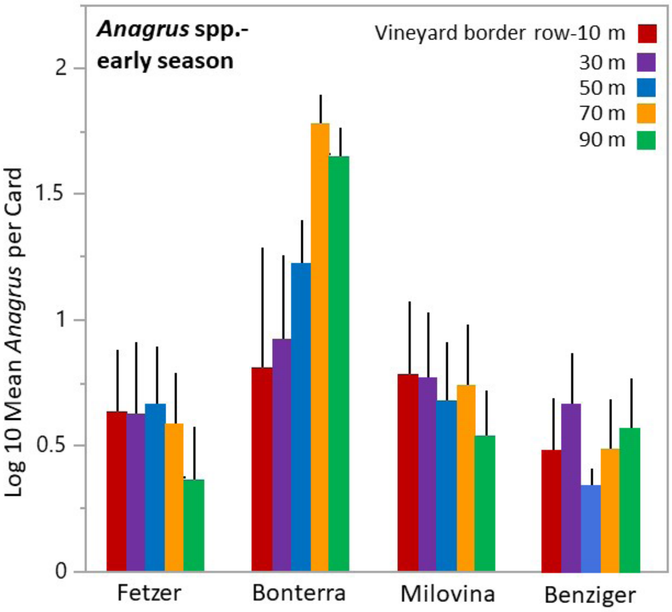

FIGURE 3
Mean early season *Anagrus* spp. density (log10 mean ± standard error of the mean) by site and distance. At Bonterra density in the border plot was 54.5% lower than the 70 m plot (p = 0.022).

of variability explained, but no significant relationship for the second leafhopper generation (p = 0.602) (Fig. 8).

There was no significant relationship between *L. mali* density and leafhopper nymphal density for the first leafhopper generation (p = 0.15), but there was a positive relationship in the second leafhopper generation (y = -0.13 + 3.01x), with 67% of the variability explained by the model (Fig. 9).

DISCUSSION

This study provides evidence that a vegetationally diverse border can influence density of WGLH and *Anagrus* spp., supporting the studies of Wilson *et al.* (2015a, 2015b, 2017) and Nichols *et al.* (2001). Several responses were revealed when the data were analyzed by site, leafhopper generation or time of the season. First, leafhopper nymphal density in both generations was significantly affected by the hedgerow at Bonterra: compared to the other sampling distances,

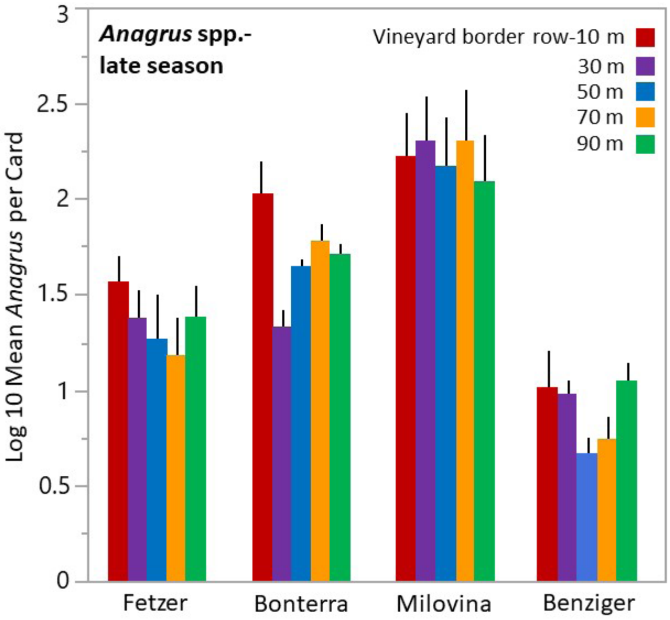

FIGURE 4

Mean late season *Anagrus* spp. density (log10 mean ± standard error of the mean) by site and distance. Across all sites, density in the border plot was 17.2% higher than in the 30 m plot (p = 0.01) and 32.8% higher than in the 50 m plot (p = 0.018).

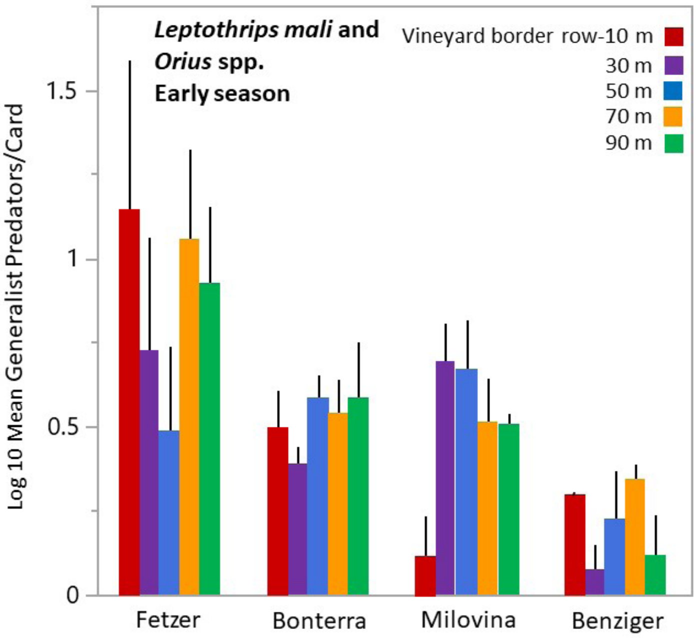

FIGURE 5

Mean early season density of *Leptothrips mali* and *Orius* spp. (log10 mean ± standard error of the mean) by site and distance. There was no significant effect of border vegetation on these generalist predators.

leafhopper density was lowest nearest the border in the first generation, but highest in the second generation. In similar studies, Wilson *et al.* (2015a) found lower density of first generation nymphs adjacent to a riparian border and Nicholls *et al.* (2001) found lower density of second generation nymphs adjacent to a flowering hedgerow. Also, at Bonterra (hedgerow) and Fetzer (riparian) it is interesting that the effect on leafhopper density in the vineyard border row was consistent between generations: at all other sampling distances, leafhopper density declined from first to second generation. This was not the case at Milovina (low-diversity tree row), where leafhopper density declined from first to second generations at all distances. The explanation for this generational decline is not known, but the results provide additional evidence that a diverse vegetational border can impact leafhopper populations. Secondly, the only early season effect on *Anagrus* spp. was at Bonterra (hedgerow), with density highest in the plots *farthest away* from the border. This finding runs counter to the concept that *Anagrus* spp. migration from its overwintering habitat would produce a density gradient (Doutt and Nakata, 1965; Murphy *et al.* 1996, 1998), resulting in highest *Anagrus* spp. activity on vines closest to the overwintering refuge, as found by Corbett and Rosenheim (1996). It is possible that in the current study the vegetational border produced a windstream that carried *Anagrus* spp. away from the margins and farther into the vineyard. Finally, there was a trend toward higher late season density of *Anagrus* spp. nearest the border (at Bonterra [hedgerow], Fetzer [riparian] and Benziger [shelterbelt], but not at Milovina [low-diversity tree row]). Interestingly, Wilson *et al.* (2017) also found a seasonal effect of non-crop vegetation (within vineyard flowering cover crops) on *Anagrus* spp. density, the effect being positive early season, but with no late season effect. In the current study, the high late season *Anagrus* spp. density in the vineyard border plot was not likely due to the border vegetation, since at that point in the season conditions and resources for this parasitoid are largely met within the vineyard.

None of these findings suggest that the influence of the vegetational border on *Anagrus* spp. explained leafhopper abundance: the seasonal patterns of *Anagrus* spp. and leafhopper abundance at Bonterra (hedgerow)

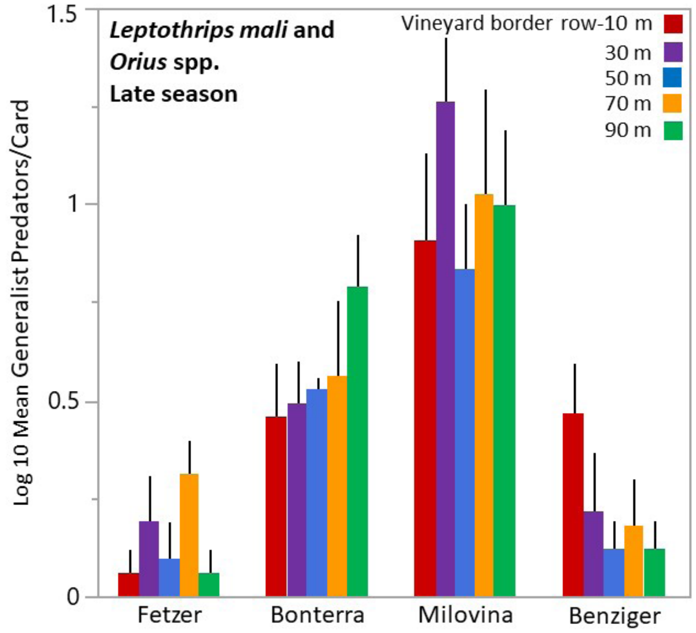

FIGURE 6

Mean late season density of *Leptothrips mali* and *Orius* spp. (log10 mean ± standard error of the mean) by site and distance. There was no significant effect of border vegetation on these generalist predators.

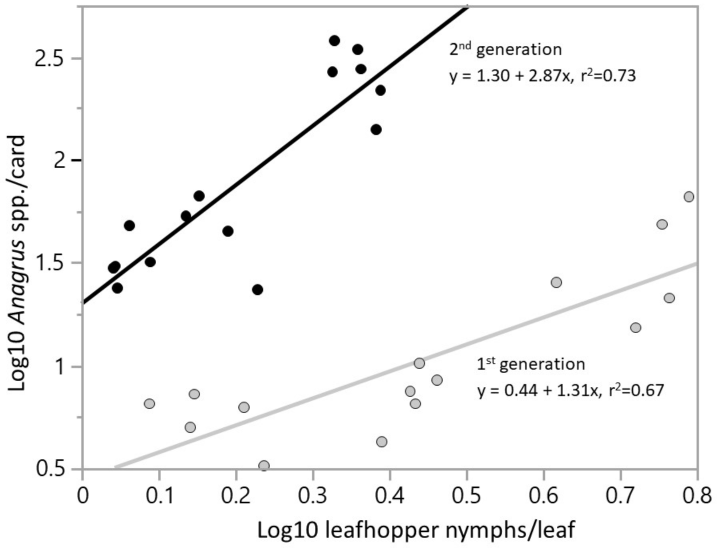

FIGURE 7

Regression of log10 *Anagrus* spp. density against log10 leafhopper nymphal density for the first (gray regression line) and second (black regression line) leafhopper generations. The regressions were positive and significant ($p<0.05$).

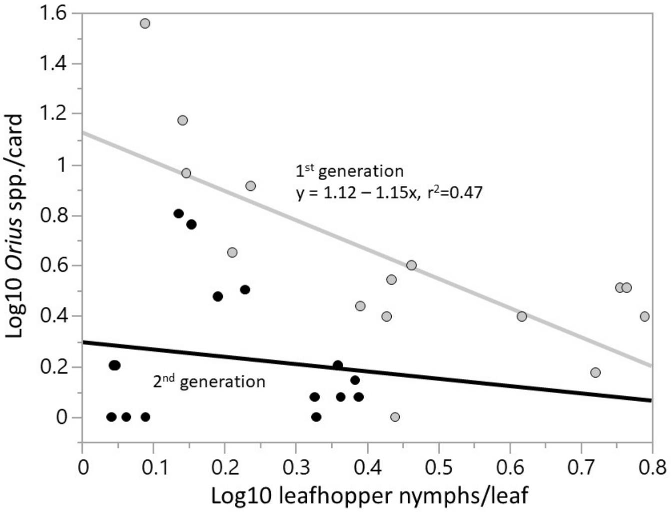

FIGURE 8
Regression of log10 *Orius* spp. density against log10 leafhopper nymphal density for leafhopper generations one (gray regression line, negatively significant at p = 0.003) and two (black regression line, not significant at p = 0.602).

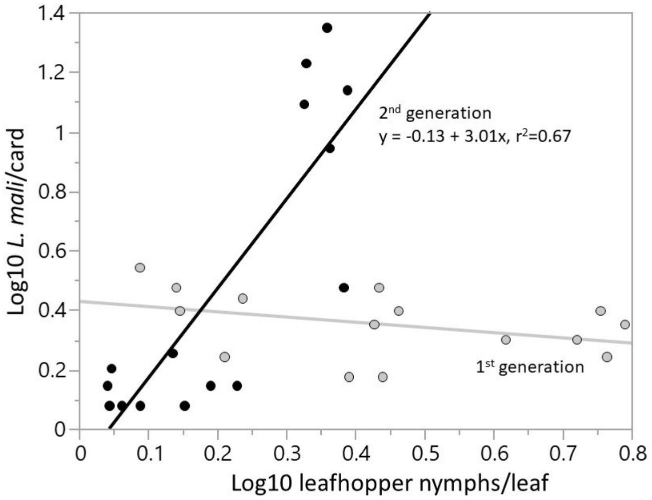

FIGURE 9
Regression of log10 *Leptothrips mali* density against log10 leafhopper nymphal density for leafhopper generations one (gray regression line, not significant at p = 0.156) and two (black regression line, positively significant at p<0.001).

were in opposition, and the overall trend toward higher late season *Anagrus* spp. density in the border plot did not correspond to lower leafhopper density. It appears then, that the primary influence of the vegetational borders was on leafhopper density, and that the pattern of *Anagrus* spp. was due to a density dependent response to the leafhoppers. This is evidenced in the regressions of *Anagrus* spp. against leafhopper density, which were significantly positive in both generations, and explained a relatively high percentage of variability (67% and 73% in the first and second generations, respectively, Fig. 7). Likewise, Nicholls *et al.* (2001) and Wilson *et al.* (2015a) found a pattern of higher leafhopper nymphal density and corresponding parasitism by *Anagrus* spp. (in each of these studies the effect was in the vineyard interior rather than the vines closest to border vegetation), which also suggests a density dependent response. Therefore, what seems to best explain *Anagrus* spp. abundance with respect to border vegetation is an indirect effect, the functional and numerical responses to WGLH density (which was affected by the vegetational border), rather than a direct influence.

In the current study there was no significant effect of the vegetational borders on the generalist predators analyzed, namely *L. mali* and *Orius* spp. Nicholls *et al.* (2001) attributed lower leafhopper density on vines near a vegetational corridor to the predatory impact of Coccinellidae, Syrphidae, Chrysopidae, Nabidae and, within the Anthocoridae, *Orius* spp. However, this conclusion does not appear to be justified, given that one of these families (the Syrphidae) does not feed on WGLH, three of them (Coccinellidae, Chrysopidae and Nabidae) are rarely if ever observed feeding on WGLH nymphs, and, with the exception of *Orius* spp., these natural enemy groups are typically found at such low densities in California vineyards (Costello & Daane, 1999) that they likely have little to no significant effect on population suppression of WGLH. Wilson *et al.* (2015a) found a late season response to the border by *Orius* spp., but admitted that the relatively low density of these predators made it difficult for the authors to analyze the data, much less conclude that generalist natural enemies played a role in leafhopper density. Whereas at our field sites *L. mali* and *Orius* spp. reached densities per card comparable to *Anagrus* spp. (e.g., Fetzer [riparian] early season, Fig. 5, and Milovina [low-diversity tree row] late season, Fig. 6), it is not clear they had an impact on leafhopper density. In fact, regression analysis showed a negative relationship between *Orius* spp. and first generation leafhopper density, and no significant relationship in the second generation, suggesting that these predators had little impact on the leafhopper population. Interestingly, Wilson *et al.* (2017) found a negative relationship between early season *Orius* spp. density and leafhopper abundance, although the trend reversed in the late season. And, although in our study there was a positive relationship between *L. mali* and second generation leafhopper density, *L. mali* is primarily known as a mite predator and pollen feeder (Parella *et al.*, 1982), and there have been no recorded observations of this thrips species feeding on *E. elegantula* nymphs; therefore its impact on leafhopper population density is uncertain.

If the effect of the vegetational border on leafhopper populations in the current study was not due to natural enemies, what might explain it? Wilson *et al.* (2015a) suggested that decreased vigor of the border vines led to lower leafhopper oviposition. It is well known that leafhoppers are sensitive to vine water status (Daane & Williams, 2003) and lay fewer eggs on water stressed vines (Costello, 2008), and therefore competition for water with the non vine vegetation could have increased water stress of the border vines. It is also possible that root associations, or additional amounts of shade at the vegetative borders, could have influenced border plot vines, which lead to vine physical or chemistry differences, affecting leafhopper oviposition or nymphal survivorship. In the current study, vine status differences could explain the lower early season leafhopper density in the border plot at Bonterra (hedgerow), and even at Fetzer (riparian), which, although not significantly different, shows the same trend. And, the fact that at Bonterra (hedgerow) leafhopper density declined from first to second generations at all distances except the border plot (and although not statistically significant, the trend was the same at Fetzer [riparian]), suggests that border plot vines were distinct from the rest of the vineyard, leading to differences in leafhopper density.

The results of this study do not lead us to conclude that vegetative corridors, borders or shelterbelts cannot influence *Anagrus* spp. density in nearby vineyards. Known *Anagrus* spp. overwintering host plants include *Rubus* spp. and *Prunus* spp. (Doutt & Nakata, 1965; Kido *et al.*, 1984), as well as *Salix* spp. and *Rosa* spp. (Wright & James, 2007; Prischmann *et al.*, 2007). In addition, some nectar bearing plants appear to enhance *Anagrus* spp. populations: Wilson *et al.* (2017) found that flowering cover crops (*Phacelia tanacetifolia, Ammi majus* and *Daucus carota*) increased early season *Anagrus* spp. density, and we found similar results with a cover crop of alyssum (*Lobularia maritima*) (Costello, Thrupp & McGourty, unpublished data). Wilson *et al.* (2016) found high winter and spring abundance of *Anagrus* spp. on the perennial *Baccharis pilularis*, which produces abundant nectar. We agree with Wilson *et al.* (2016) that the impact of alternative vegetation on *Anagrus* spp. will depend on the type and frequency of favored *Anagrus* spp. host plants in the vegetational border or corridor. *Baccharis pilularis* was not present at any of our sites, and although *Rubus procerus* and *Rosa multiflora* were present in the native border at our Fetzer (riparian) site, they may not have been present in high enough density to augment early season *Anagrus* spp. density in the vineyard.

CONCLUSIONS

Our results show that there can be an effect of border vegetation on vineyard leafhopper populations, which support findings in similar studies. In our study, at two sites with a diverse vegetative border, the result was a fairly stable seasonal population of leafhoppers in the vineyard border rows, whereas otherwise leafhopper density decreased between the first and second generations, and this effect was not seen at the low-diversity vegetation border site. Our results provide no evidence that the impact of the border vegetation was on *Anagrus* spp. or generalist predators, rather, they suggest that the border vegetation had an undetermined influence on vine condition in the border rows, which affected leafhopper oviposition or nymphal survivorship.

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