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Influence of Landscape Diversity and Flowering Cover Crops on Biological Control of the Western Grape Leafhopper (Erythroneura elegantula Osborn) in North Coast Vineyards

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Influence of Landscape Diversity and Flowering Cover Crops on Biological Control of the Western Grape Leafhopper (*Erythroneura elegantula* Osborn) in North Coast Vineyards

by

Sam Houston Wilson Jr.

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Committee in charge:

Dr. Miguel A. Altieri, Chair
Dr. Kent M. Daane
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Abstract

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Professor Miguel A. Altieri, Chair

Modern agriculture is characterized by specialized production and the use of monoculture cropping practices. These agroecosystems are at once concentrating habitat for crop pests and eliminating habitat for natural enemies. Multiple studies have demonstrated that such changes can lead to a decrease or total loss of biological control of pests. At the same time, expansion of monoculture cropping systems across entire agricultural regions has led to the creation of landscapes that are entirely dominated by a small number of crops and devoid of natural habitats. In the same way, entire regions can experience a reduction or loss of biological control to agriculture.

As such, a number of studies have compared crop fields with high and low habitat diversity and found that diversified cropping systems tend to have enhance natural enemy populations and increased biological control of pests. At the same time, another set of studies have demonstrated that monoculture cropping systems can still experience high levels of biological control so long as they are situated in a landscape with high levels of habitat diversity surrounding them. More recently, it has been proposed that the use of on-farm habitat diversification to enhance biological control will likely be influenced by the area and quality of natural habitat surrounding the farm (i.e. landscape diversity).

This dissertation was designed to evaluate the influence of habitat diversity at the local and landscape scale on biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn; Hemiptera: Cicadellidae) in North Coast wine grape vineyards. The key parasitoids of *E. elegantula* are *Anagrus eryhthroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn (Hymenoptera: Mymaridae). These *Anagrus* parasitoids are intimately tied to the natural habitats that surround vineyards due to the fact that in order for them to successfully overwinter they must parasitize an alternate leafhopper host that overwinters in an egg stage (*E. elegantula* overwinters in the vineyard as an adult). These alternate leafhopper hosts are known to reside in the natural and semi-natural habitats that surround North Coast vineyards. As such, it is thought

that biological control of *E. elegantula* in vineyards is particularly sensitive to changes in landscape diversity. At the same time, the use of monoculture cropping practices results in a vineyard environment that is very inhospitable to natural enemies of *E. elegantula*, including *Anagrus* spp. Previous studies have demonstrated that without floral nectar (or an analogous solution) the lifespan of *Anagrus* parasitoids can be less than two days and it may be that the introduction of flowering cover crops into vineyards could possibly increase biological control of *E. elegantula* by enhancing *Anagrus* longevity in the field. In this way, increased habitat diversity at both the field and landscape scale may support increased natural enemy populations which would lead to increased biological control of *E. elegantula*.

For this dissertation, a series of studies were conducted in order to evaluate how changes in habitat diversity at the field and landscape scale could affect natural enemy populations and ultimately influence biological control of *E. elegantula*. First, overwintering habitat of *Anagrus* spp. was evaluated to identify the specific host plant species that contained leafhopper eggs that these parasitoids were attacking in natural habitats during the winter, as well as throughout the rest of the year. Second, vineyards that were adjacent to riparian habitat were studied in order to evaluate how distance away from a large natural habitat patch influenced the timing, density and impact of natural enemies in the vineyard. Third, in order to isolate the influence of landscape diversity, a multi-year study was conducted to monitor biological control of *E. elegantula* in a number of vineyard monocultures that were situated in low, intermediate and high diversity landscapes. Finally, over the course of several years the use of flowering summer cover crops was developed in collaboration with commercial wine grape growers and vineyard trials were subsequently conducted to evaluate the ability of these flowering cover crops to enhance biological control of *E. elegantula*. In order to evaluate how changes in the landscape influenced the effectiveness of this on-farm habitat diversification practice, these cover crop studies were conducted at multiple vineyards that were situated in low, intermediate and high diversity landscapes.

Results from these studies indicate that the area and composition of natural habitats surrounding vineyards can have a significant influence on biological control of *E. elegantula*. Reduced pest populations in more diverse landscapes is thought to be the result of both reduced crop vigor as well as increased natural enemy impact during the overwintering period. Early season populations of *Anagrus* wasps were found in all vineyards regardless of landscape diversity, implying a strong dispersal capacity from overwintering sites. The *Anagrus* demonstrated a strong density dependent relationship with *E. elegantula* and this appeared to drive their densities in vineyards much more so than changes in landscape diversity.

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Acknowledgements

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Chapter 1: Introduction

Anthropogenic land-use conversion has reduced the area and connectivity of natural habitats on a global scale (Tilman et al. 2001, Foley et al. 2005) and this has led to significant biodiversity loss across multiple taxa (Sala et al. 2000, Cushman 2006), including arthropods (Didham et al. 1996). Biodiversity declines are generally accompanied by decreases in overall ecosystem function (Daily 1997, Hooper et al. 2005) and in particular a loss of ecosystem services to agriculture (Matson et al. 1997), including biological control of pests (Tscharntke et al. 2005, Bianchi et al. 2006).

One of the primary drivers of land use conversion is agriculture (Foley et al. 2005). Modern agriculture is characterized by specialized crop production systems that are largely based in the use of monoculture cropping practices (Gleissman 2007). By maximizing the area devoted to a single crop species, resources for key phytophagous pests of these crops are highly concentrated in one particular area which allows them to more easily locate, colonize and proliferate in crop fields. At the same time, these simplified cropping systems lack many of the resources required to support natural enemies of crop pests, including refugia and overwintering sites, alternate hosts for parasitoids and alternate prey for predators, as well as nectar and pollen resources (Russell 1989, Landis et al. 2000). Working in combination, the simultaneous concentration of habitat for pests and elimination of habitat for their natural enemies can lead to reductions in the biological control of pests and increased pest outbreaks (Root 1973, Letourneau 1987).

The problems association with field scale crop simplification can be extended to a much larger spatial scale as well. As the development of monoculture cropping systems expands throughout an entire agricultural region, vast areas of land can become dominated by a small number of crop species and at the same time be devoid of natural habitats that can provide resources to support natural enemies of crop pests (Kruess and Tscharntke 1994, Duelli and Obrist 2003). Similar to what occurs at the field scale, the regional concentration of plant-host resources for phytophagous pests paired with the elimination of non-crop resources to support natural enemies can also lead to reductions in the biological control of crop pests (Tscharntke et al. 2005, Bianchi et al. 2006).

In a majority of these cases, reductions or total loss of biological control in agriculture has been remedied by the use of insecticides. While many of these products were initially very effective and affordable, their continued use in the future is currently in question. Over the past 40 years there has been a growing body of literature documenting the alarmingly negative environmental and human health impacts associated with the use of insecticides (Eskanazi et al. 2007, Geiger et al. 2010). Such documented effects have led to the restriction, regulation or outright prohibition of many of these products (FQPA 1996). Additionally, consumer demand for insecticide-free food products is on the rise (Yiridoe et al. 2005). Pesticide efficacy is in decline as well, as there are now more than 500 insect species that are reported with resistance to insecticides (Whalon et

al. 2008). Finally, rising energy prices are likely going to drive up the cost of insecticide production and application, both of which will make chemical control less affordable to growers.

In response to these problems, a number of chemical companies have tried to reduce insecticide exposure to non-target organisms by developing insecticides with new chemistries and selective modes of action (e.g., neonicotinoids, systemics) as well as genetically engineer specific crops to contain bacterium (such as *Bacillus thuringiensis* Berliner 1915) in their plant tissue that is toxic to certain insect pests (Casida 2012, Sanahuja et al. 2011). For their part, many growers have also adopted integrated pest management practices and made significant efforts to adjust equipment and application timing in order to reduce pesticide drift as well as adopt better safety practices in order to reduce farm worker exposure (Warner 2007).

Alternately, there has been growing interest amongst growers, scientists, policy-makers and consumers in the development and use of ecologically-based pest management practices in agriculture (National Research Council 1996). Ecologically-based pest management is a form of conservation biological control which seeks to support and enhance the natural enemies of crop pests through on-farm habitat diversification and management (Altieri et al. 1983, Altieri and Nicholls 2004, Gurr et al. 2004).

Many studies have evaluated the use of on-farm habitat diversification to enhance biological control of pests (Letourneau et al. 2011). Diversified cropping systems can take a variety of forms, from simply increasing genetic diversity of a single productive crop species to intercropping multiple crop and non-crop species (Pickett and Bugg 1998, Altieri and Nicholls 2004, Gurr et al. 2004). For the most part, research to evaluate the influence of habitat diversity on biological control in agriculture has focused on the addition of non-crop species into crop monocultures. For example, studies have evaluated the role of overwintering habitat (Thomas et al. 1992, Macleod et al. 2004), cover cropping (Bugg and Waddington 1994), floral resource provisioning (Hickman and Wratten 1996, Berndt et al. 2006, Lee and Heimpel 2008), semi-natural hedgerows (Morandin et al. 2011), and weedy vegetation (Altieri and Whitcomb 1980, Norris 1982). Reviews of this work have shown that while diversified cropping systems can in some cases enhance natural enemy populations and biological control of pests, as well as crop quality and yield, overall results have been fairly mixed (Andow 1991, Tonhasca and Byrne 1994, Letourneau et al. 2011). Furthermore, regardless of whether or not crop diversification led to an increase in biological control, the ecological mechanisms responsible for these outcomes is not always clear and a number of competing hypotheses have been suggested (see Poveda et al. 2008 for a review).

While researchers previously hypothesized that changes in landscape-scale habitat diversity could have a significant impact on biological control (van Emden 1965), it is only more recently that studies have been conducted to address this relationship empirically. Many of the studies to address the influence of landscape diversity on biological control are by nature observational rather than manipulative, given the difficulty of establishing experimental treatments at such a large spatial scale. Such studies have typically monitored natural enemy populations and/or

biological control of pests at multiple field sites situated along a gradient of landscape-scale habitat diversity (Marino and Landis 1996, Thies and Tscharntke 1999, Gardiner et al. 2009). These studies usually quantify ecological features within a 1-3 km radius around a crop field, although some studies have measured landscape features at scales ranging from as little as 0.2 km to at most 25 km (Thies and Tschantke 1999, Ostman et al. 2001, Steffan-Dewenter et al. 2002, Isaia et al. 2006). Landscape diversity is generally quantified in terms of the relative proportion of various habitat types within a given area (e.g., 32% oak woodland within a 1.5 km radius of a crop field), although some studies have used a diversity index of habitat types (e.g., Simpsons, Shannon-Weaver etc.) or simply utilize categorical terms to describe a landscape (e.g., "complex" and "simple" landscapes) (Thies and Tscharntke 1999, Isaia et al. 2006, Gardiner et al. 2009, Chaplin-Kramer and Kremen 2012).

Similar to the results of the field-scale diversification studies, reviews of landscape-scale studies have shown that although farms located in agricultural landscapes with high levels of habitat diversity tend to have increased natural enemy populations, this does not consistently lead to increased biological control of pests (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). Again, a number of different hypotheses have been proposed to explain these inconsistent outcomes (see Chaplin-Kramer et al. 2011 for a review).

The ability of on-farm habitat diversification practices to enhance natural enemy populations and biological control of pests is likely dependent on landscape context. The idea that the addition of supplemental resources to a cropping system will necessarily attract natural enemies of crop pests relies on the assumption that a larger, more regional population of natural enemies (i.e., a metapopulation) actually exists to begin with (Tscharntke et al. 2007). The persistence of a viable natural enemy metapopulation is contingent on the size, arrangement and connectivity of suitable habitat as well as the probability of extinction and dispersal capacity of these organisms (Hanski 1998). For natural enemies of crop pests in highly disturbed agricultural systems dominated by monoculture, such habitat likely consists of the natural and semi-natural areas that surround crop fields. These habitats can effectively act as source-pools of natural enemies that have the potential to seasonally colonize crop fields and/or recolonize them following localized extinctions (Duelli et al. 1990, Tscharntke and Brandl 2004). In agricultural regions where these habitats have been mostly eliminated, the minimum area of suitable habitat (Hanski et al. 1996) necessary to support a metapopulation of natural enemies may not exist and in such situations the addition of on-farm habitat to support natural enemies will, at best, be met with little success and, at worst, lead to false conclusions about the ability of on-farm habitat diversity to enhance biological control.

A few studies have begun to evaluate how changes in habitat diversity at the field- and landscape-scale interact. These projects typically compare paired control and treatment plots at multiple field sites that are situated along a gradient of landscape diversity. To date, a majority of these studies have evaluated how changes in landscape diversity influence biological control on organic versus conventional farms (Letourneau and Goldstein 2001, Ostman et al. 2001, Clough et al. 2005, Roschewitz et al. 2005, Eilers and Klein 2009) while relatively fewer studies have compared

simplified and diversified plots across multiple landscapes (Haenke et al. 2009, Chaplin-Kramer and Kremen 2012). Similar to previous habitat diversification studies, results have been mixed. In some cases the performance of on-farm practices were outweighed by the influence of the landscape (Ostman et al. 2001, Clough et al. 2005 Roschewitz et al. 2005, Haenke et al. 2009) while in other studies the two factors worked in conjunction (Eilers and Klein 2009, Chaplin-Kramer and Kremen 2012) or there was no clear influence of habitat diversity at either scale (Letourneau and Goldstein 2001). As such, much remains to be known about the ways in which these localized, on-farm habitat diversification practices function in various types of low and high diversity landscapes.

This dissertation project was the result of a multi-year collaboration with commercial wine grape growers in Napa and Sonoma County who were interested in the development of ecologically-based pest management practices. In particular, the growers were interested in the use of flowering summer cover crops as a means of increasing habitat diversity to enhance biological control of pests.

From 2008-2009, we worked with a group of eight growers to trial a number of flowering cover crops in their vineyards. These pilot studies consisted of non-replicated split-plot trials in which a plot with flowering cover crops was compared to a plot without the flowers. Flower species used in these pilot studies included annual buckwheat (*Fagopyrum esculentum* Moench), sweet alyssum (*Lobularia maritima* [L.] Desv.), lacy phacelia (*Phacelia tanacetifolia* Benth.) and crimson clover (*Trifolium incarnatum* L.). These flowering cover crop species were initially selected based on their previous use in vineyards and/or successful enhancement of biological control in other cropping systems. Over the course of these pilot studies we monitored development of the flowers in the vineyard as well as collected data on natural enemy and pest abundance.

During these and all of the subsequent pilot studies, we facilitated a number of cross-visits amongst the participating growers in order to give them a chance to see how the flowers were doing in other vineyards and to exchange information with each other about the establishment and management of flowering cover crops. We would also typically give a short presentation at these events that provided an overview of the scientific evidence to date regarding habitat diversification to enhance biological control in agriculture. These events were a great way for us to reiterate our thoughts and perspectives as well as receive feedback from the growers on the goals and objectives of this project.

Results from the 2008-2009 pilot studies indicated that the plots with flowering cover crops typically had increased natural enemy populations and decreased pest populations. Unfortunately, buckwheat, sweet alyssum and crimson clover were also all determined to be agronomically incompatible for use in vineyards. Flowers that needed to be sown in the spring were difficult for growers to establish because they could only be sown once the soil was dry enough to support a tractor driving over it (typically 15 April) but before the last spring rains occurred (typically 15 May). Targeting such a narrow window of time, especially given all of the other tasks required of growers at this time of the year, proved very difficult. Additionally, these

flowers were all very sensitive to water stress and could not live beyond June 1 without supplemental irrigation, which was entirely out of the question due to the costs and limitations of the water supply. Furthermore, irrigation systems would need to be modified in order to deliver water to the row middles. While some vineyards did use overhead sprinklers for frost protection, a majority of the research sites relied on drip irrigation that could not be easily redirected to the row middles.

Given these limiting factors, we began to search for other flowering cover crop species that were fall sown and drought tolerant for subsequent trials in 2010 and 2011. Ultimately we identified bullwort (*Ammi majus* L.) and wild carrot (*Daucus carota* L.) to compliment the early season *P. tanacetifolia* bloom. The use of bullwort (*Ammi majus* L.) was essentially the result of a mistake. It was sold to one of the participating growers as "Queen Anne's Lace", which turned out to be the common name for both *Ammi majus* L. and *Daucus carota* L. The grower was under the impression that this was *D. carota* and we were all surprised when the *A. majus* appeared in late May. The timing of the bloom was excellent, coming up just after the *P. tanacetifolia* declined, and the flowers harbored an abundant and diverse natural enemy population. The wild carrot (*Daucus carota* L.) was hidden in plain sight. Throughout these pilot studies Albie Miles and I had spent countless hours driving around Napa and Sonoma County to collect samples at the various field sites and during these trips we spent a fair amount of time brainstorming various flower species for use in the vineyards. Finding a flower that could provide a bloom in the late summer period had proven especially vexing and we had practically run out of ideas when it dawned upon Albie that we could possibly make use of the wild carrot that grew along the roadsides near the vineyards. The irony is that throughout our earlier conversations in the car there were endless blooms of wild carrot streaming past us. Sweep net sampling revealed that indeed this flower was very attractive to a number of beneficial insects, especially *Orius* sp., and the timing of the wild carrot bloom coincided well with the decline of the *A. majus*. We were concerned that ordering wild carrot seed from a commercial seed house may provide us with a cultivar that was selected for garden conditions (i.e., required irrigation) and so over the course of this project all of the wild carrot seed used in the experiments was harvested by hand from stands growing along the side of the road.

The pilot studies in 2010-2011 primarily focused on fine-tuning the establishment and management of the three flower species *P. tanacetifolia*, *A. majus* and *D. carota*. The flowers did best when sown earlier in the fall prior to the first winter rains, although some growers were able to put them in as late as January and still get a good stand of flowers that year. The small size of the flower seeds made it difficult to sow them evenly with a seed drill and many of the growers found that this could be alleviated by blending the seed with rice hulls or bran. Sowing the flowers to the entire width of the row middle was another problem, as the tall stands of flowers interfered with workers trying to manage the vine canopy and/or machinery that was trying to pass down the row. The solution to this was to sow the flowers in a tight strip down the center of the row middles, which created a passable space between the flower strip and the vine canopy. All of these adjustments improved the flowering cover crop treatment and made it more

amenable to a wider variety of vineyard conditions. Ultimately, this allowed for the establishment of a fairly uniform set of field trials during the 2012-2013 cover cropping study.

This dissertation was designed to evaluate how changes in habitat diversity at multiple spatial scales influence biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn) by its key parasitoids *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn. As previously discussed, it has been shown that changes in habitat diversity at the local and landscape scale can both have an influence on biological control. More importantly, it has been hypothesized that the ability of localized, on-farm habitat diversification to enhance biological control may be contingent upon the diversity of the landscape the farm is situated in. We thought this was especially likely to occur in the wine grape system given that the *Anagrus* wasps attacking *E. elegantula* in vineyards required overwintering sites that are located in patches of natural habitat outside of the vineyard (Doutt and Nakata 1965a, Lowery et al. 2007, Daane et al. 2013). Thus when we began our collaboration with growers in Napa and Sonoma we decided that it would be necessary to address the influence of landscape diversity as part of our work to develop and evaluate the use of flowering cover crops to enhance biological control in vineyards. The individual dissertation chapters can roughly be broken into a series of questions that address the relationship between habitat diversity and biological control of *E. elegantula* by *Anagrus* spp.

What are the specific host plants utilized by *Anagrus* spp. in the landscape?
Chapter One addresses an important question about the quality of habitats at the landscape scale. While it is known that in order to successfully overwinter the *Anagrus* wasps must parasitize alternate leafhopper hosts that overwinter in an egg stage and that these alternate hosts are most likely located in the natural and semi-natural habitats outside of vineyards, the specific plant hosts that these leafhoppers reside on are unknown in the North Coast. This information is critical to our understanding of how changes in the arrangement and composition of natural habitats at the landscape scale influence the timing and abundance of *Anagrus* wasp activity in vineyards. Results from this study highlight the importance of conserving and promoting functional biodiversity as versus biodiversity *per se* in vineyards.

To what extent do biological control services extend out from patches of natural habitat?
A key question that I frequently hear raised by growers and scientists alike has to do with the spatial arrangement of habitat diversity in and around crop fields. This has been a source of debate in the conservation biology community for decades concerning the use of “single large” or “several small” (SLOSS) habitat preserves (Simberloff 2010). With regards to biological control of pests, if we know that patches of natural habitats are serving as source pools of natural enemies in agroecosystems, then what is the ideal spatial arrangement of these patches? How much vineyard can we contiguously plant before a patch of habitat is needed to break up the monoculture and provide support for natural enemies? The study in Chapter Two is an attempt to address these questions by studying the timing and spatial extent of natural enemy and pest densities in vineyards adjacent to large patches of riparian habitat.

What is the influence of landscape diversity on biological control in vineyards?
In order to tease apart the effects of landscape and local habitat diversity, we decided to first conduct a study that would evaluate biological control in vineyard monocultures situated in low, intermediate and high diversity landscapes. If we want to understand how the landscape mediates the effects of on-farm diversification practices, it would be important to first isolate the influence of landscape diversity itself in vineyard monoculture.

The study presented in Chapter Three was one of the more ambitious sampling efforts that was conducted for this dissertation, as we collected data at more than 30 vineyard sites over the course of four years. Aside from the large, if at times unwieldy, dataset that was produced from this study, working on this component of the dissertation really gave me a chance to experience the amazing diversity of vineyard operations in the North Coast as well as gain a sense of the year-to-year variability in biological control at these sites.

Does landscape diversity mediate the ability of flowering cover crops to enhance biological control?
Chapter Four is in many ways the grand finale of this dissertation project. I first became excited about the idea of trialing the flowering cover crops across a continuum of landscape diversity after reading my first papers on the possible interactions between local and landscape diversity during an informal seminar on agroecology that was organized by graduate students Albie Miles and Nathan McClintock in the fall of 2007. Mixed results from previous studies evaluating on-farm habitat diversification to enhance biological control may have partially been due to the fact that landscape diversity at the study site was never accounted for although we know that this can have an effect on the ability of such practices to enhance biological control. As such, it was important for us to test these cover cropping practices in a variety of vineyard landscape types.

It is worthwhile to note that countless hours went into the prerequisite work for the study presented in Chapter Four and it was only after years of trial and error that we were able to successfully develop and establish a fairly uniform flowering cover crop treatment at multiple field sites across Napa and Sonoma County in 2012-2013. Asking a grower to let you sample insects in their vineyard is one thing, but asking them to establish and manage a novel and very particular cover crop treatment is a whole other task. Ensuring the uniformity of these trials took endless hours of coordination and site visits with the growers.

We inevitably lost trial sites due to poor treatment establishment, as some growers that were new to the project had less experience sowing the small-seeded flowers in their vineyards. This was partially remedied by a grower-mentorship program that we setup to pair new project participants with collaborating growers who had been working with the flowering cover crops for many years. The experienced growers could then provide advice, guidance, and even equipment to those who were just getting started with this type of summer cover cropping. Communication issues also led to some lost trials. For example, we had a site where a miscommunication between management and the field crew led to the entire experiment being plowed under by mistake. In some other cases the problem was too many flowers rather than too few, as a few collaborating

growers were sometimes apt to toss in a few extra flower species along with the three that were part of the experimental treatment. Although it was done with the best of intentions, the additional flower species confounded the experimental design. Finally, there were also a number of more idiosyncratic problems. For instance, at one site the vineyard owners were reluctant to mow the *P. tanacetifolia* after it had bloomed because they enjoyed looking at the flowers when they walked their dogs past the experimental block each morning. Luckily in this case the management was able to convince them of the need to mow and the trial was saved. At another site, the *P. tanacetifolia* was actually mowed early because the vineyard owners did not enjoy the color of the flowers (which are purple, just like the red wine they produced…I couldn't figure this one out). I could go on with stories like this, but the point is that it took a lot of energy to run these trials at such a diverse array of vineyard sites.

Chapter 2: Overwintering habitat of *Anagrus* spp. (Hymenoptera: Mymaridae)

ABSTRACT

Anagrus wasps are the key parasitoids of the Western grape leafhopper (*Erythroneura elegantula* Osborn) in Northern California wine grape vineyards. While *E. elegantula* overwinters as an adult in reproductive diapause, *Anagrus* wasps must locate an alternate leafhopper host that overwinters in an egg stage that they can parasitize in order to successfully overwinter. These alternate leafhopper hosts are thought to be primarily located in the natural and semi-natural habitats surrounding vineyards. This study sought to identify the plants that serve as hosts for the alternate leafhoppers that *Anagrus* wasps parasitize in order to overwinter. Over the course of two years, samples of plant material from the various plant species that comprise the natural and semi-natural habitats surrounding vineyards were collected and brought to the greenhouse in order to rear out overwintering *Anagrus* wasps. Results from this study indicate that *Anagrus* are attacking leafhopper eggs on specific host plants in these habitats and that in some cases leafhoppers on these plants serve as hosts for the wasps not just in the winter, but throughout the entire year.

INTRODUCTION

The western grape leafhopper (*Erythroneura elegantula* Osborn; Hemiptera: Cicadellidae) is a common pest of wine grapes in Northern California and the greater Pacific Northwest (Daane et al. 2013). *Erythroneura elegantula* adults feed and reproduce on grape leaves throughout the grape growing season (March – October), typically completing 2-3 generations per year in this region. Feeding by *E. elegantula* causes leaf stippling which reduces vine productivity through a decrease in photosynthesis and can lead to reduced crop yield and quality. High populations of *E. elegantula* adults in the fall can also be a nuisance to workers harvesting grapes. As grape vine leaves begin to senesce and drop from the vine in mid-October, *E. elegantula* adults move onto the vineyard floor or out of the vineyard where they overwinter in reproductive diapause on grasses, weedy vegetation or perennial evergreen plants, such as citrus. In spring, as grape vines begin to produce new shoots and leaves, the adults move back onto the grape vines to feed and deposit eggs (Daane et al. 2013).

The key parasitoids of *E. elegantula* are *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn (Hymenoptera: Mymaridae). Both wasps attack the eggs of *E. elegantula* throughout the grape growing season. Whereas *E. elegantula* overwinter as adults, *Anagrus* wasps overwinter in host eggs and are thus required to seek out alternate leafhopper host species that overwinter as eggs in order to successfully overwinter (Doutt and Nakata 1965). These alternate hosts are thought to reside in the natural and semi-natural habitats that are often found near vineyards (Doutt and Nakata 1965, Kido et al. 1984, Lowery et al. 2007).

Previous studies have identified a number of plant species, and in some cases even the alternate leafhopper host species, which *Anagrus* wasps utilize to overwinter. Doutt and Nakata (1965, 1966, 1973) observed that vineyards adjacent to stands of wild blackberry (*Rubus* spp.) had greater early season populations of *Anagrus* (at that time referred to as *Anagrus epos* Girault) as well as increased *E. elegantula* egg parasitism rates, presumably due to the increased availability of *Anagrus* overwintering habitat. Their work indicated that the alternate leafhopper host was the blackberry leafhopper (*Dikrella californica* Lawson). Kido et al. (1983) observed a similar relationship in vineyards adjacent to French prune orchards and, similar to the previous work on blackberries, proposed that *Anagrus* was overwintering in the eggs of the prune leafhopper (*Edwardsiana prunicola* Edwards) in these trees (Kido et al. 1984, Wilson et al. 1989). Based on the findings of these initial studies it was recommended that grape growers establish stands of wild blackberry and/or French prune adjacent to their vineyards in order to enhance biological control of *E. elegantula*, although this was met with limited success (Flaherty et al. 1985; Murphy et al. 1996, 1998a, 1998b)

A major revision to the description of *Anagrus* occurred in the 1990s, when a global survey on the systematics of the genus *Anagrus* revealed that a number of unique species were being referred to as *A. epos* (Triapitsyn 1998). For instance, re-examination of voucher specimens from the Doutt and Nakata work found that what was described as *A. epos* reared from *D. californica*

on wild blackberry and *E. elegantula* on cultivated grape were actually two different species, *A. daanei* Triapitsyn (commonly reared from *D. californica*) and *A. erythroneurae* S. Trjapitzin & Chiappini (commonly reared from *E. elegantula* and *Erythroneura variabilis* Beamer on grape) (Trjapitzin 1995). Although both of these species are known to attack *E. elegantula*, it confounded conclusions from earlier studies that the *Anagrus* wasps overwintering on blackberry were the same as those attacking *E. elegantula* in vineyards. Furthermore, these findings may explain why previous attempts to augment *Anagrus* overwintering habitat by planting either blackberries or prunes near vineyards were not entirely successful, as these plants may have been supporting populations of an *Anagrus* species that was not actually the dominant species attacking leafhoppers in vineyards.

Subsequent to the revisions by Triapitsyn (1998), further studies to identify *Anagrus* overwintering habitat have been conducted in New York (Williams and Martinson 2000), Washington and Oregon (Wright and James 2007) and British Columbia (Lowery and Triapitsyn 2007). In a related effort, Prischmann et al. (2007) identified the *Anagrus* species attacking *E. elegantula* and *E. ziczac* Walsh (Virginia creeper leafhopper) in Washington and Oregon vineyards.

While both *A. erythroneurae* and *A. daanei* are present in Northern California vineyards, not much is known about their overwintering habitat preferences in this region. Although many of the overwintering leafhopper hosts and host-plants identified in previous surveys can be found in this area, there are a number of plant species unique to the region that have never been surveyed (such as *Baccharis pilularis* DC., *Ceanothus* spp., and *Aesculus californica* [Spach] Nutt.). As such, a survey was conducted in 2012-2014 to identify *Anagrus* overwintering habitat in California's North Coast wine grape growing region as well as evaluate the seasonal timing that the wasps utilize this habitat.

METHODS

Study sites consisted of at least 12 separate patches (>400 m^2) of natural and semi-natural habitats found near vineyards in Napa and Sonoma County, California, USA. The primary natural habitats sampled were oak woodland and riparian, which are the dominant natural habitats in this study region. Semi-natural habitats such as hedgerows and gardens adjacent to vineyards were also included in the survey. From January - May of 2012 and January 2013 – January 2014, vegetation was sampled every 4 weeks from the various plant species that comprised these natural and semi-natural habitats. *Anagrus* wasps were reared following methods adapted from Lowery et al. (2007). Plant material was brought to the greenhouse, weighed and then placed into opaque cylindrical paper cartons and held under controlled conditions (24^{o}C, 16:8 h [L:D] cycle, 40% RH) for 4 weeks to encourage the emergence of any overwintering *Anagrus* wasps. A glass vial was secured to the top of the container to allow light to enter the chamber and attract emerging wasps. Emergence chambers were checked daily. All emerging adult *Anagrus* were

collected and stored in 95% EtOH. All specimens were then sent to Dr. Serguei Triapitsyn (UC Riverside) for identification.

RESULTS

Over the course of this entire survey 1,118 collections of plant material were made from 76 unique plant species found in and around North Coast vineyards. A total of 1,787 *Anagrus* specimens were reared from 20 plant genera across 13 different families (Table 2.1, Figure 2.1). *Anagus* species collected in this survey include *A. atomus* L., *A. avalae* Soyka, *A. daanei*, *A. erythroneurae*, *A. nigriventris* Girault and *A. tretiakovae* Triapitsyn. Some wasps were able to be identified only to genus (*Anagrus* sp.) or species group ("*A. atomus* group" = *A. erythroneurae, A. ustulatus* Haliday, and *A. atomus*; "*A. incarnatus* group" = *A. epos, A. daanei, A. tretiakovae,* and *A. incarnates* Haliday).

The 20 host plant genera from which *Anagrus* were reared are listed as either "cultivated" or "natural" to indicate the nature of their presence in this region (Table 2.3, Figures 2.2 and 2.3). Natural plant species are those naturally occurring in the study region and are the result of little to no human intervention. Cultivated plants are those species typically intentionally managed in a hedgerow, garden or some other form of aesthetic and/or productive planting near vineyards. This distinction serves to differentiate novel host plant species from those that are likely responsible for maintaining *Anagrus* populations on a regional scale.

Species and host plant association are shown in terms of total wasps per gram of plant material sampled ($x10^{-3}$) over the course of this survey. While this metric is surely not a perfect correlate of total plant surface area and/or host abundance, it is simply intended to provide a rough estimate of parasitoid density on the vegetation sampled from the different host plants.

Data on the timing of *Anagrus* host-plant use is provided in Table 2.2. Many *Anagrus* species emerged from plant material collected throughout the year rather than just during the overwintering period when grape vines were dormant (Table 2.2). The four time periods are listed as "winter" (December – February), "spring transition" (March – May), "summer" (June – August), and "fall transition" (September – November). These designations are based upon the seasonal ecology of *Anagrus* wasps and wine grape phenology rather than the calendar-based seasons.

Slide-mounted voucher specimens of the *Anagrus* wasps identified in this study were deposited in the Entomology Research Museum, University of California, Riverside, CA, USA.

Table 2.1 *Anagrus* spp. host plant associations

Family	Common Name	Species Name	*Anagrus* Species	Wasps/gram ($x10^{-3}$)
Apocynaceae	Periwinkle	*Vinca major*	*A. nigriventris*	4.4
Asteraceae	Coyotebrush	*Baccharis pilularis*	*Anagrus.* sp.	1.5
			A. atomus	1.1
			A. sp. *atomus* group	1.2
			A. erythroneurae	18.9
			A. sp. *incarnatus* group	1.5
Betulaceae	Alder	*Alnus rhombifolia*	*Anagrus.* sp.	3.4
			A. atomus	3.7
			A. sp. *atomus* group	4.3
			A. avalae	3.4
			A. erythroneurae	3.2
			A. sp. *incarnatus* group	1.4
Ericaceae	Manzanita	*Arctostaphylos* sp.	*A. erythroneurae*	1.9
Fagaceae	Coast live oak	*Quercus agrifolia*	*A.* sp. *atomus* group	0.7
			A. erythroneurae	0.7
Lamiaceae	Catnip	*Nepeta* sp.	*Anagrus* sp.	5.3
			A. atomus	17.7
			A. sp. *atomus* group	16.7
			A. erythroneurae	166.0
	Lavender	*Lavendula* sp.	*A. atomus*	5.7
	Mint	*Mentha* sp.	*Anagrus* sp.	1.7
			A. atomus	6.6
			A. sp. *atomus* group	5.1
			A. erythroneurae	65.9
	Sage	*Salvia* spp.	*A. atomus*	4.5
			A. sp. *atomus* group	2.3
			A. erythroneurae	33.9
Lauraceae	California bay	*Umbellularia californica*	*Anagrus* sp.	5.4
			A. sp. *atomus* group	5.0
Rhamnaceae	Ceanothus	*Ceanothus* spp.	*Anagrus* sp.	1.6
			A. sp. *atomus* group	9.0

			A. erythroneurae	26.0
			A. tretiakovae	12.4
Rosaceae	Apple	*Malus* sp.	*A.* sp. *atomus* group	2.8
			A. erythroneurae	3.0
	Blackberry	*Rubus* sp.	*Anagrus* sp.	5.3
			A. atomus	6.4
			A. sp. *atomus* group	11.5
			A. daanei	3.3
			A. erythroneurae	12.0
			A. sp. *incarnatus* group	5.2
			A. nigriventris	2.3
			A. new sp. *atomus* group	3.3
			A. new sp. *incarnatus* group	4.4
	Rose	*Rosa* spp.	*A. atomus*	0.6
			A. sp. *atomus* group	1.5
			A. daanei	1.5
			A. sp. *incarnatus* group	1.5
			A. nigriventris	1.7
	Toyon	*Heteromeles arbutifolia*	*A.* sp. *atomus* group	2.2
Rutaceae	Citrus	*Citrus* sp.	*A.* sp. *atomus* group	6.1
Salicaceae	Poplar	*Populus* sp.	*A.* sp. *atomus* group	5.7
			A. sp. *incarnatus* group	2.9
	Willow	*Salix* spp.	*Anagrus* sp.	5.5
			A. sp. *atomus* group	2.4
			A. sp. *incarnatus* group	12.9
			A. new sp. *atomus* group	18.9
Sapindaceae	California buckeye	*Aesculus californica*	*Anagrus* sp.	1.4
			A. atomus	1.5
			A. sp. *atomus* group	1.7
			A. erythroneurae	2.0
			A. sp. *incarnatus* group	1.2
			A. nigriventris	2.4
Vitaceae	Wild grape	*Vitis californica*	*A. atomus*	2.2

			A. sp. *atomus* group	2.3
			A. daanei	5.3
			A. erythroneurae	4.8
	Wine grape	*Vitis vinifera*	*A. erythroneurae*	-
			A. daanei	-

Table 2.2 Seasonality of *Anagrus* spp. host plant use

Common Name	**Species Name**	***Anagrus* Species**	**Win**	**Spr**	**Sum**	**Fal**
Periwinkle	*Vinca major*	*A. nigriventris*	X			
Coyotebrush	*Baccharis pilularis*	*Anagrus* sp.	X			
		A. atomus	X			
		A. sp. *atomus* group	X	X	X	
		A. erythroneurae	X	X	X	X
		A. sp. *incarnatus* group	X			
Alder	*Alnus rhombifolia*	*Anagrus* sp.		X	X	X
		A. atomus			X	
		A. sp. *atomus* group	X	X	X	X
		A. avalae	X	X	X	X
		A. erythroneurae		X	X	
		A. sp. *incarnatus* group			X	X
Manzanita	*Arctostaphylos* sp.	*A. erythroneurae*	X			
Coast live oak	*Quercus agrifolia*	*A.* sp. *atomus* group		X		
		A. erythroneurae		X		
Catnip	*Nepeta* sp.	*Anagrus* sp.	X	X		
		A. atomus	X	X	X	X
		A. sp. *atomus* group	X	X	X	X
		A. erythroneurae	X	X	X	X
Lavender	*Lavendula* sp.	*A. atomus*		X	X	
Mint	*Mentha* sp.	*Anagrus* sp.		X	X	
		A. atomus		X	X	X
		A. sp. *atomus* group		X	X	X
		A. erythroneurae		X	X	X
Sage	*Salvia* spp.	*A. atomus*	X	X	X	
		A. sp. *atomus* group	X		X	
		A. erythroneurae	X	X	X	X
California bay	*Umbellularia californica*	*Anagrus* sp.	X			
		A. sp. *atomus* group			X	
Ceanothus	*Ceanothus* spp.	*Anagrus* sp.		X		
		A. sp. *atomus* group	X	X	X	X
		A. erythroneurae	X	X	X	X

		A. tretiakovae				X
Apple	*Malus* sp.	*A.* sp. *atomus* group			X	X
		A. erythroneurae				X
Blackberry	*Rubus* sp.	*Anagrus* sp.	X			X
		A. atomus	X	X	X	X
		A. sp. *atomus* group	X	X	X	X
		A. daanei				X
		A. erythroneurae	X	X	X	X
		A. sp. *incarnatus* group	X		X	
		A. nigriventris	X	X		
		A. new sp. *atomus* group				X
		A. new sp. *incarnatus* group			X	
Rose	*Rosa* spp.	*A. atomus*	X			
		A. sp. *atomus* group				X
		A. daanei				X
		A. sp. *incarnatus* group				X
		A. nigriventris			X	
Toyon	*Heteromeles arbutifolia*	*A.* sp. *atomus* group	X			
Citrus	*Citrus* sp.	*A*. sp. *atomus* group			X	
Poplar	*Populus* sp.	*A.* sp. *atomus* group			X	
		A. sp. *incarnatus* group			X	
Willow	*Salix* spp.	*Anagrus* sp.				
		A. sp. *atomus* group			X	
		A. sp. *incarnatus* group			X	X
		A. new sp. *atomus* group			X	X
California buckeye	*Aesculus californica*	*Anagrus* sp.		X	X	
		A. atomus		X		
		A. sp. *atomus* group		X		
		A. erythroneurae		X		
		A. sp. incarnatus group			X	
		A. nigriventris		X		
Wild grape	*Vitis californica*	*A. atomus*				X
		A. sp. *atomus* group				X
		A. daanei				X
		A. erythroneurae			X	X

Table 2.3 Host plant typology

Distribution	Family	Common Name	Species Names
Natural	Apocynaceae	Periwinkle	*Vinca major*
	Asteraceae	Coyotebrush	*Baccharis pilularis*
	Betulaceae	Alder	*Alnus rhombifolia*
	Ericaceae	Manzanita	*Arctostaphylos* spp.
	Fagaceae	Coast live oak	*Quercus agrifolia*
	Lauraceae	California bay	*Umbellularia californica*
	Rosaceae	Blackberry	*Rubus* spp.
		Toyon	*Heteromeles arbutifolia*
	Salicaceae	Poplar	*Populus* sp.
		Willow	*Salix* spp.
	Sapindaceae	California buckeye	*Aesculus californica*
	Vitaceae	Wild grape	*Vitis californica*
Cultivated	Lamiaceae	Catnip	*Nepeta* sp.
		Lavender	*Lavendula* sp.
		Mint	*Mentha* sp.
		Sage	*Salvia* sp.
	Rhamnaceae	Ceanothus	*Ceanothus* spp.
	Rosaceae	Apple	*Malus* sp.
		Rose	*Rosa* spp.
	Rutaceae	Citrus	*Citrus* sp.

Figure 2.1 Proportional abundance of *Anagrus* species reared from cultivated and natural host plant species

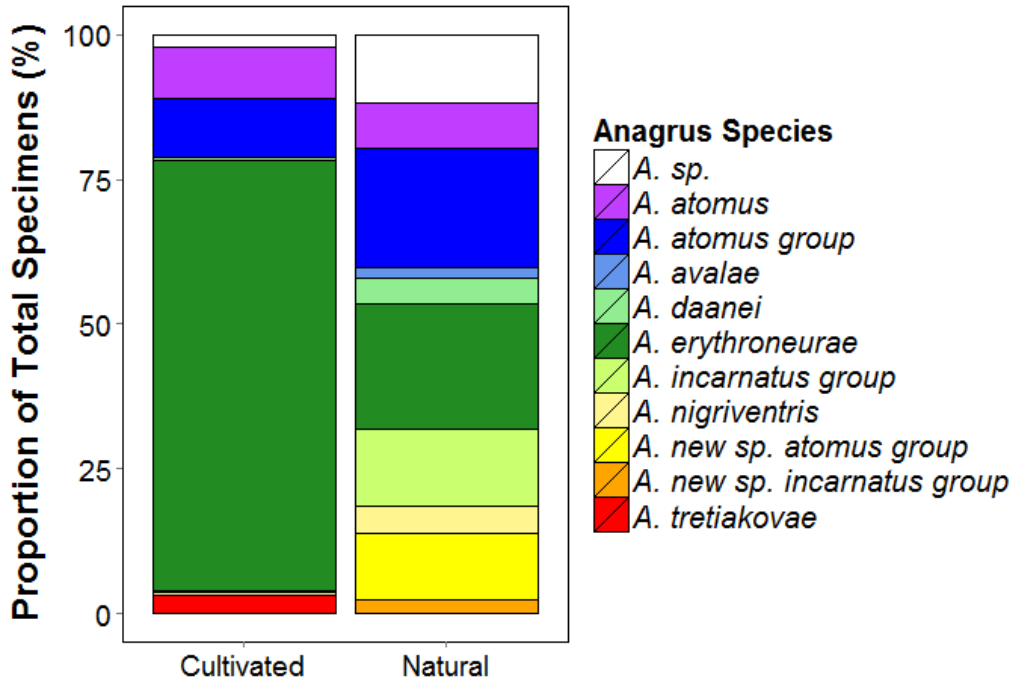


Figure 2.2 Proportional abundance of *Anagrus daanei* and *Anagrus erythroneurae* on host plants from natural habitats.

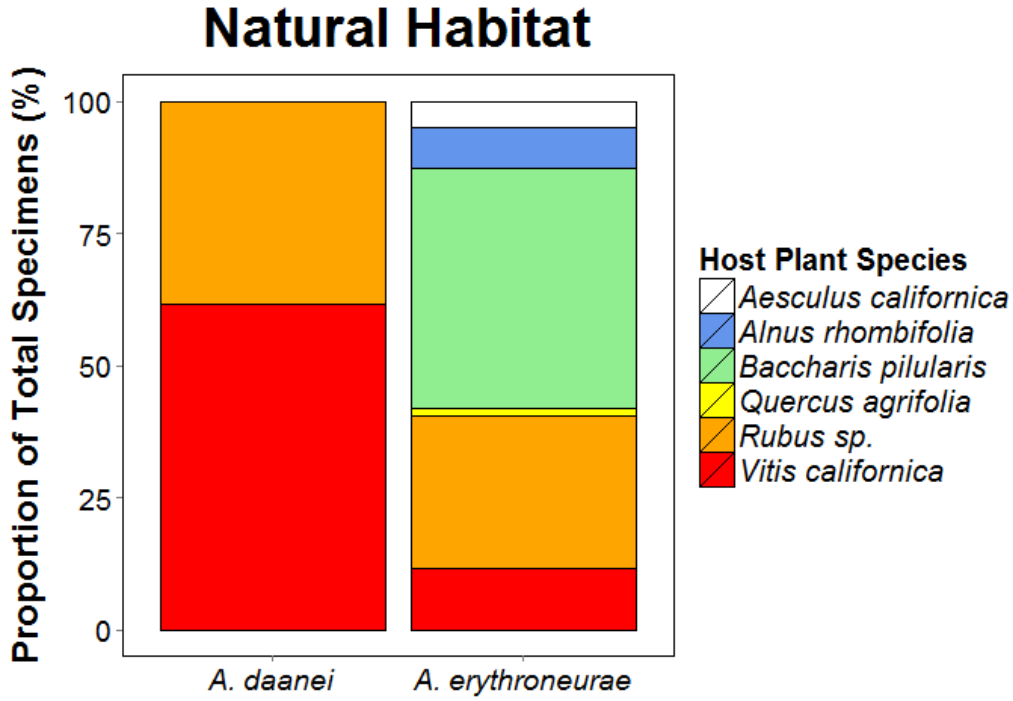
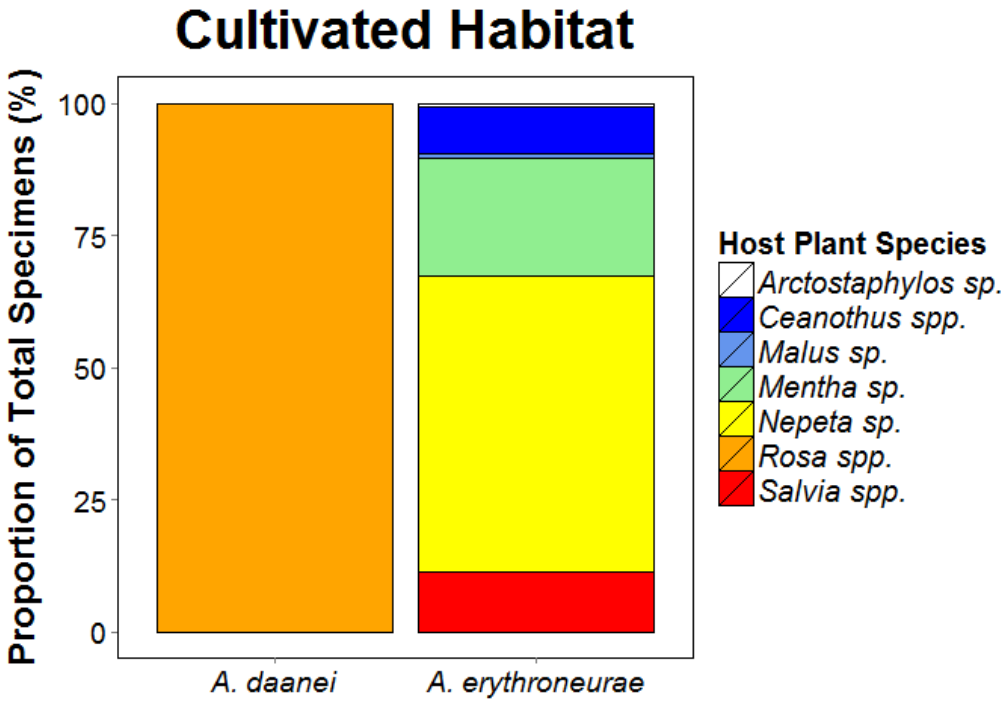


Figure 2.3 Proportional abundance of *Anagrus daanei* and *Anagrus erythroneurae* on host plants from cultivated habitats.



DISCUSSION

This survey both confirmed results from previous studies of *Anagrus* host-plant associations as well as identified a number of new and novel hosts. Host plant families that have not previously been reported include Apocynaceae, Asteraceae, Ericaceae, Lauraceae, Rhamnaceae, and Sapindaceae; genera include *Arctostaphylos*, *Umbellularia*, *Ceanothus*, *Heteromeles*, *Populus*, and *Aesculus*; and species include *Baccharis pilularis*, *Aesculus californica*, *Vinca major*, *Umbellularia californica*, and *Heteromeles arbutifolia*. The dominant *Anagrus* species identified in this survey were *A. erythroeneura* and *A. atomus*, while *A. daanei*, *A. avalae*, *A. nigriventris* and *A. tretiakovae* were far less frequently encountered. Two of these species are key parasitoids of *E. elegantula*, they are *A. erythroneurae* and *A. daanei*.

Anagrus erythroneurae was collected from leafhoppers on 12 species or genera from 9 different families. Specimens primarily came from *Nepeta* sp., *Mentha* sp., *Salvia* sp., *Baccharis pilularis* and *Rubus* sp. Most of the host-plant associations match with previous Nearctic surveys (Triapitsyn 1998, Williams and Martinson 2000, Wright and James 2007, Lowery et al. 2007), although *B. pilularis*, *Arctostaphylos* spp. and *Ceanothus* spp. are all new records for this species. A survey in British Colombia collected *A. erythroneurae* from *Cornus stolonifera* as well (Lowery et al. 2007).

Anagrus atomus was reared from 10 species or genera from 6 different families. It was primarily collected from *Nepeta* sp., *Mentha* sp., *Rubus* sp., *Lavendula* sp., and *Salvia* spp. *Baccharis pilularis* and *Aesculus californica* are both new host-plant records for *A. atomus*. *Alnus* sp. is also a new record, although *A. atomus* has been collected from other genera in the Betulaceae, including *Betula* spp. and *Ostrya* sp. (Lowery et al. 2007, Williams and Martinson 2000). While *A. atomus* is commonly found attacking *Empoasca* spp. leafhoppers on grape vines (Vitaceae) in Europe and Asia (Chiappini et al. 1996, Triapitsyn and Berezovskiy 2004), in the Nearctic region it is primarily limited to the Rosaceae where it has been documented attacking *Typhlocyba pomaria* (McAtee) and *Empoasca maligna* Woodworth (on *Malus* spp.), *Edwardsiana prunicola* (on *Rosa* sp. and *Prunus* sp.), and *Dikrella* sp. (on *Rubus* sp.) (Triapitsyn 1998).

Anagrus avalae was collected from only one plant species, *Alnus rhombifolia*. Similar to *A. atomus*, this is a new host-plant record but a previous survey in British Columbia found this species on another plant in the same family, *Betula occidentalis* (Lowery et al. 2007). *Anagrus atomus* can be found throughout western North America as well as southeast Canada and is known to attack a number of leafhoppers on plants in the Rosaceae, including *Edwardsiana rosae* on *Rosa* sp., *E. prunicola* on *Prunus* sp., and *Typhlocyba pomaria* on *Malus* spp. (Triapitsyn 1998, Lowery et al. 2007, Wright and James 2007).

Anagrus daanei was reared from only three hosts in two families. While this species is commonly found attacking *E. elegantula* in North Coast wine grape vineyards, outside of the vineyard it could only be found on *Vitis californica*, *Rubus* sp. and *Rosa* sp. *Anagrus daanei* has previously been documented attacking *Erythroneura* leafhoppers in Washington state and British Columbia (Lowery et al. 2007, Prischmann et al. 2007). In western North America, *A. daanei* has also been found on *Prunus* sp. (Triapitsyn 1998) and *Parthenocissus quinquefolia* (Lowery et al. 2007). Surveys in the eastern United States have collected *A. daanei* from leafhopper eggs on the plant species *Acer saccarum*, *Robinia pseudoacacia*, and *Zanthoxylum americanum* as well (Williams and Martinson 2000).

Anagrus nigriventris was encountered on four plants in three families, including *Vinca major*, *Aesculus californica*, *Rubus* sp. and *Rosa* sp. Both *V. major* and *A. californica* are new host-plant associations for this species. Previous surveys have identified *A. nigriventris* attacking *Erythroneura* leafhoppers on grape in New York state as well as on leafhopper eggs on the host plant *Robinia pseudoacacia* (Williams and Martinson 2000). In California, Oregon and Washington it has been reared from leafhopper eggs from *Rubus* sp. in multiple surveys (Wright and James 2007, Triapitsyn 1998, Lowery et al. 2007).

Anagrus tretiakovae was collected only from leafhoppers on *Ceanothus* spp., but this represents both a new host-plant association as well as the first time this species has been found in California. *A. tretiakovae* has previously been found attacking *Erythroneura* leafhoppers on grape in New York state (Williams and Martinson 2000), Washington (Prischmann et al. 2007) as well as in the southwest United States (Triapitsyn 1998). This species has also been collected from a number of plant-hosts in the Rosaceae in Oregon and Washington (Wright and James 2007).

While records on the timing of host plant use are not absolute due to differences in sampling effort, some conclusions can still be inferred. Certain *Anagrus* species appeared to make use of leafhoppers on specific host-plants throughout the majority of the year. This includes *A. erythroneurae* on *B. pilularis*, *Ceanothus* spp., *Rubus* sp., *Nepeta* sp., and *Salvia* sp.; *A. atomus* from *Mentha* sp., *Rubus* sp., *Nepeta* sp., and *Salvia* sp.; and *A. avalae* from *Alnus rhombifolia*, its only documented host in this survey.

The more cryptic species that were documented on these plants are likely able to utilize them throughout the year, but were only found in certain periods due to their low overall abundance. This includes *A. daanei* and *A. nigriventris* on *Rubus* sp. and *A. tretiakovae* on *Ceanothus* spp.

Anagrus nigriventris was collected from *V. major* and *Rosa* spp. in the "winter" and "summer" respectively, but no conclusions can be drawn as to how frequently this species rely on these hosts due to the limited number of specimens reared from either of these plants.

Alternately, some host-plants truly appeared to be utilized only during very specific periods of the year, such as *A. atomus*, *A. erythroneurae* and *A. nigriventris* on *A. californica* in March – May and *A. atomus, A. erythroneurae* and *A. daanei* on *V. californica* in August – November. Both of these plant species are deciduous and although they were sampled multiple times throughout the year *Anagrus* specimens were only ever reared during very specific windows of time that coincided with the presence of leaves on these plants. This is especially true for *A. californica*, which has a very narrow window of time during which leaves are present (typically March – May, though foliage can remain present until as late as August where soil moisture is very high)

In a similar manner, while *A. avalae* was collected from *A. rhombifolia* throughout the entire year, *A. atomus* and *A. erythroneurae* were collected from this host-plant only between March – August. *Alnus rhombifolia* is winter deciduous and thus collections of *A. avalae* between December – February indicate the likely use of a leafhopper host that deposits eggs into the woody material of the plant while *A. atomus* and *A. erythroneurae* (collected only in the spring/summer when leaves are present) are suspected of attacking leafhopper host eggs found on the leaves.

Anagrus erythroneurae and *A. daanei* are the key egg parasitoids of *E. elegantula* in North Coast wine grape vineyards and arguably the most important natural enemy for biological control of this pest. While large quantities of *A. erythroneurae* emerged from *Nepeta*, *Mentha* and *Salvia* collections, it is thought that *B. pilularis* and *Rubus* sp. are the primary overwintering host-plants supporting regional populations of this parasitoid, through the leafhopper eggs present on these host plants, as these two plants can be widely found throughout the North Coast region. *Baccharis pilularis* is a drought-tolerant woody perennial shrub and is typically found growing in field margins, along road ways, and in other disturbed habitats. While *Rubus* sp. is more restricted to riparian areas, it can thrive outside of these areas given the proper soil moisture requirements and is therefore also found along drainage ditches and in low-lying pasture. In a similar fashion,

out of the three *A. daanei* host-plants documented in this survey, *Rubus* sp. is likely the key species supporting regional *A. daanei* populations. The other two host-plants (*Rosa* sp. and *V. californica*) are either restricted in their abundance (*Rosa* sp., mostly found in small-scale, aesthetic plantings) or serve as a suitable plant host only in the summer and fall when foliage is present (*V. californica*, which is winter deciduous). As mentioned, *Rubus* sp. is widely abundant throughout the North Coast and has foliage throughout the entirety of the year.

Originally, Doutt and Nakata (1965, 1973) outlined a two-phase cycle in which *Anagrus* parasitoids were primarily found in commercial grape vineyards attacking *E. elegantula* throughout the growing season (April – October) but when the grape vines lose their leaves and go dormant (November – March) the *Anagrus* migrate over to another plant species and attack an alternate leafhopper host in order to successfully overwinter.

While this is generally accurate, it is likely that *A. erythroneurae* and *A. daanei* make use of a number of intermediate host-plants during their seasonal migration between commercial vineyards and overwintering habitat. The year can thus be divided into 4 phases rather than 2. These phases are listed in Table 2 as “winter”, “spring transition”, “summer” and “fall transition”. A similar process was suggested by Cerutti et al. (1991) for *A. atomus* attacking *Empoasca vitis* (Göthe) in European vineyards.

While no data exist specifically for *A. erythroneurae* and *A. daanei*, previous studies have indicated a lower developmental threshold of 7.2°C for *A. epos* (Williams 1984) and 8.39°C for *A. atomus* (Agboka et al. 2004). Average air temperature in the North Coast typically only falls below these thresholds during the months of December – February (CIMIS 2014). Grape vine development has a lower threshold of 10°C (Williams et al. 1985). In North Coast vineyards the first fully-expanded mature grape leaves generally do not appear until mid-April, at which point *E. elegantula* begin to lay eggs into the leaf material. As such, elevated regional temperatures in early March likely trigger the development and emergence of overwintering *Anagrus* wasps. Since suitable host sites (i.e., leafhopper eggs) are not present on commercial grape vines until late April or early May, these parasitoids most likely complete at least one or more full generations on an alternate/intermediate host during the March-April period before moving into vineyards. Similarly, in late August when the photophase drops below 13.6 hours, *E. elegantula* enter into reproductive diapause and cease to oviposit onto grape leaves (Cate 1975), forcing *A. erythroneurae* and *A. daanei* to seek out alternate hosts outside of the vineyard. Again, because average temperatures remain above developmental thresholds for these parasitoids until December, they likely complete one or more generations on alternate/intermediate hosts during the September-November period before finally settling onto their overwintering host for the December-February period.

While alternate host-plants are critical for the support of overwintering populations of *A. erythroneurae* and *A. daanei*, they also appear to provide refugia for these parasitoids throughout the year. While both *A. erythroneurae* and *A. daanei* were consistently observed attacking *E. elegantula* in vineyards during the summer, these parasitoids were simultaneously

collected from a number of alternate host-plants, including *B. pilularis*, *Rubus* sp., *Salvia* sp. and *Nepeta* sp., *Ceanothus* sp. This indicates that some portion of the population remains outside of the vineyard throughout the year, even when *E. elegantula* are active on wine grapes. These alternate host-plants likely serve as refugia when vineyard conditions become inhospitable for the *Anagrus* (i.e., low/no *E. elegantula* population, die off from mistimed chemical spray, lack of water or floral resources) and/or provide individuals to re-colonize vineyards following a localized reduction in the *Anagrus* population.

Results from this survey provided new information on the use of alternate leafhopper species from host plants by a number of *Anagrus* wasp species in the North Coast. Since both *A. erythroneurae* and *A. daanei* are known to attack *E. elegantula*, identification of their alternate host plants has implications for the use of on-farm habitat diversification practices to enhance biological control of this pest in wine grape vineyards. For example, growers could potentially augment habitat in and around their vineyard with the plant species identified in this survey that were shown to be hosts for *A. daanei* and *A. erythroneurae*. Alternately, preexisting natural habitats could be managed to promote the growth of overwintering host plants for these two *Anagrus* species as well.

Future research should focus on the timing and movement of *Anagrus* wasps between various alternate host plants and vineyard habitats as well as seek to identify the insects being parasitized by *Anagrus* wasps on these host plants. This latter fact is key in developing a better understanding of both leafhopper species and their host plant use by *Anagrus* and will be needed to test the manipulation of *Anagrus* numbers through hedgerow plantings. Further insight into the ecology of these wasps could potentially aid in the development of more reliable conservation biological control programs for control of *E. elegantula* in commercial wine grape vineyards.

Chapter 3: Vineyard proximity to riparian habitat is associated with changes in crop vigor, leafhopper egg deposition and nymph abundance

ABSTRACT

This study was conducted in order to evaluate how vineyard proximity to riparian habitat influences biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn; Hemiptera: Cicadellidae). Natural enemy and pest populations, as well as pest parasitism rates, were monitored over a two-year period at multiple vineyard sites adjacent to riparian habitat. At each site, pest and natural enemy data were collected along a transect that extended out from the riparian habitat into the vineyard. Follow-up work at a subset of the original research sites evaluated differences in crop vigor, pest abundance and parasitism rates between the vineyard edge and interior. Findings from this study indicated that vineyard areas closer to riparian habitat had lower crop vigor as well as reduced *E. elegantula* egg deposition and nymph abundance. Since natural enemy populations and parasitism rates did not demonstrate any consistent spatial trends relative to the riparian habitat, it was concluded that *E. elegantula* preference for more vigorous vines, rather than natural enemy impact, was responsible for the observed differences in egg deposition and nymph abundance between vines at the vineyard edge and interior.

INTRODUCTION

Anthropogenic land-use conversion has reduced the area and connectivity of natural habitats on a global scale (Tilman et al. 2001, Foley et al. 2005) and this has led to significant biodiversity loss across multiple taxa (Sala et al. 2000, Cushman 2006), including arthropods (Didham et al. 1996). Biodiversity declines are generally accompanied by decreases in overall ecosystem function (Daily 1997, Hooper et al. 2005) and in particular a loss of ecosystem services to agriculture (Matson et al. 1997), including biological control of pests (Tscharntke et al. 2005, Bianchi et al. 2006).

Habitat fragmentation (as versus outright habitat loss) can also influence biodiversity and ecosystem function (Fahrig 2003, Ries et al. 2004, Fischer and Lindemayer 2007). In a landscape dominated by agricultural production, small fragments or patches of natural habitat can serve as reservoirs of biodiversity (Tscharntke and Brandl 2004) which could potentially provide a source population of natural enemies to seasonally colonize crop fields (Duelli 1990, Thomas et al. 1991, Ekbom et al. 2000, Pfiffner and Luka 2000, Duelli and Obrist 2003). In this way, proximity to patches of natural habitat may influence the timing and abundance of natural enemies migrating into a cropping system and subsequent biological control of crop pests (Tscharntke et al. 2005). Patches of natural habitat adjacent to cropping systems can also provide supplementary resources absent from the cropping system that can benefit natural enemies, such as nectar, pollen, alternate prey/hosts and refugia (Landis et al. 2000).

Many studies have found that crops adjacent to patches of natural habitat have increased natural enemy populations (Kajak and Lukasiewicz 1994, Pfiffner and Luka 2000, Schmidt and Tscharntke 2005, Oberg and Eckbom 2006, Sackett et al. 2009), decreased pest populations (Nicholls et al. 2001, Paredes et al. 2013) and increased natural enemy impacts on pests (Altieri and Schmidt 1986, Tscharntke et al. 2002, Thomson and Hoffman 2009). Of course, species response to edge habitats will likely vary according to the life history of the organism and/or the plant species composition of the edge habitat (Tscharntke and Brandl 2004). As such, there are some examples where crops adjacent to habitat edges were unaffected (D'Alberto et al. 2012) or even experienced an increase in pest population (English-Loeb et al. 2003)

The development and expansion of wine grape production in California's North Coast region over the past 40 years has led to the creation of an agricultural landscape dominated by vineyards with natural habitats that are relatively small in area and highly fragmented (Hilty and Merenlender 2004). The Western grape leafhopper (*Erythroneura elegantula* Osborn; Hemiptera: Cicadellidae) is a key pest of wine grapes in California and the greater Pacific Northwest. *Erythroneura elegantula* feeds and reproduces on grape leaves throughout the grape growing season (typically from April to October for most North American wine grapes) and then overwinters as an adult in a reproductive diapause in leaf litter and on weedy or perennial vegetation near the vineyard (Daane et al. 2013). Feeding by *E. elegantula* causes leaf stippling that reduces vine productivity and can ultimately affect crop yield and quality. Spiders are the primary generalist predator of vineyard *Erythroneura* species, and they comprise more than 90%

of the predator community in vineyards (Costello and Daane 1995, 1999). Other predators that attack *E. elegantula* include Cantharidae, *Orius* sp., *Chrysoperla* sp., *Hippodamia convergens* (Guérin-Méneville), *Geocoris* sp., *Hemerobius* sp., *Nabis* sp., and Syrphidae (Daane et al. 2013). The key parasitoids of *E. elegantula* are *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn (Hymenoptera: Mymaridae). These tiny (<1 mm) wasps attack the eggs of *E. elegantula* and closely related leafhopper species. A key factor for parasitism of *E. elegantula* is that this leafhopper species overwinters as an adult whereas the *Anagrus* wasps overwinter as immatures in the eggs of leafhopper species that overwinter in the egg stage (Daane et al. 2013). These alternate leafhopper host species are typically found in natural habitats outside of the vineyard (Doutt and Nakata 1965, Lowery et al. 2007).

Whereas some research has described the impact of vineyard cover cropping on spider and *Erythroneura* densities (Costello and Daane 1998, 2003) or the manipulation of *Chrysoperla* on *Erythroneura* densities (Daane et al. 1996), there are few published studies that describe the effect of surrounding landscapes on natural enemies of vineyard leafhoppers. Nicholls et al. (2001), observed that vineyard sections closer to a riparian woodland habitat had lower *E. elegantula* nymph populations and higher generalist predator (*Orius* sp. in particular) populations than sections further inside the vineyard. Similarly, Thomson and Hoffman (2013) reported increased natural enemy abundance as well as enhanced predation and parasitism rates of sentinel light-brown apple moth eggs (*Epiphyas postvittana* Walker) at vineyard edges adjacent to woody vegetation. Hogg and Daane (2010, 2011) evaluated spider abundance and species composition along a transect that extended from natural habitats (oak woodland, riparian) into adjacent vineyards. Their findings suggested that spiders were seasonally colonizing vineyards from natural habitats and discussed the implications of this for biological control (Hogg and Daane 2011). However, D'Alberto et al. (2013) monitored spider populations in vineyards adjacent to pastures and woodlots and found only a weak positive correlation between spider abundance and vineyards adjacent to pastures. Moreover, a vineyard's proximity to natural landscape was not always associated with a decrease in vineyard pest densities. Botero-Garces and Isaacs (2003, 2004) observed that uncultivated habitats adjacent to vineyards harbor grape berry moth (*Endopiza viteana* Clemens) and there was a weak but positive association between vineyard moth populations and presence of wild grapes in adjacent natural habitats.

The first studies to address the landscape influence on *Anagrus* spp. parasitism of vineyard leafhoppers were conducted by Doutt and Nakata (1965a). Their work revealed that *Anagrus* (referred to as *A. epos* Girault) overwintered on wild blackberry (*Rubus* sp.), a plant commonly encountered in riparian habitats adjacent to California vineyards (Doutt and Nakata 1965b). Subsequent studies found that *E. elegantula* egg parasitism increased with vineyard proximity to patches of *Rubus* sp. (Doutt and Nakata 1966) and leafhopper eggs in vineyards down-wind from riparian habitats experienced earlier and more frequent parasitism levels (Doutt and Nakata 1973). Ponti et al. (2003, 2005) monitored *Anagrus* populations in Italian vineyards and their adjacent hedgerows primarily containing *Rubus* sp. and *Ulmus* sp., and suggested that *Anagrus* were building up large populations in hedgerows and then seasonally colonizing vineyards. They hypothesized that *Rubus* sp. and *Ulmus* sp. served as an overwintering habitat for leafhopper

species needed for *Anagrus* overwinter survival – although details of species associations were not provided. Similarly, Williams and Martinson (2000) recorded higher *Anagrus* populations and egg-parasitism rates of *Erythroneura* leafhoppers in New York vineyards adjacent to semi-natural woodlots, and they identified a number of overwintering host plants in these same woodlots that were utilized by leafhopper species that were parasitized by *Anagrus*. However, they also report that *Erythroneura* nymph and adult populations were actually higher at the vineyard edge relative to interior vineyard sections. English-Loeb et al. (2003) also recorded higher early-season populations of *Anagrus* wasps at the vineyard edge, but parasitism rates were not significantly higher.

Riparian areas are ecologically critical habitat for a variety of both terrestrial and aquatic flora and fauna (NRCS 2007). They can serve as corridors for migrating wildlife, supply water for frost protection and crop irrigation, as well as habitat for natural enemies of vineyard pests (Doutt and Nakata 1973, Nicholls et al. 2001, Hilty and Merenlender 2004). Riparian habitats can also be detrimental to viticulture; for example, many riparian plant species are known repositories for the destructive grape vine pathogen *Xylella fastidiosa* Wells et al., the causal agent of Pierce's disease, as well as habitat for blue-green sharpshooters (*Graphocephala atropunctata* [Signoret]), a key vector of this bacterium (Purcell et al. 1998, Baumgartner et al. 2005). While many studies have evaluated natural enemy populations and biological control of pests as it relates to general landscape context (see Chaplin-Kramer et al. 2011) this study was designed to evaluate the degree to which this ecosystem service extends out from individual patches of natural habitat. Riparian habitat was chosen for this study in particular because it is one of the primary natural habitat types in this region that regularly abuts to vineyards. In this study, natural enemy and pest abundance and pest parasitism rates were monitored in multiple vineyards adjacent to patches of riparian habitat in California's North Coast wine grape region in order to determine whether or not biological control of *E. elegantula* is influenced by vineyard proximity to riparian habitat.

METHODS

Study sites

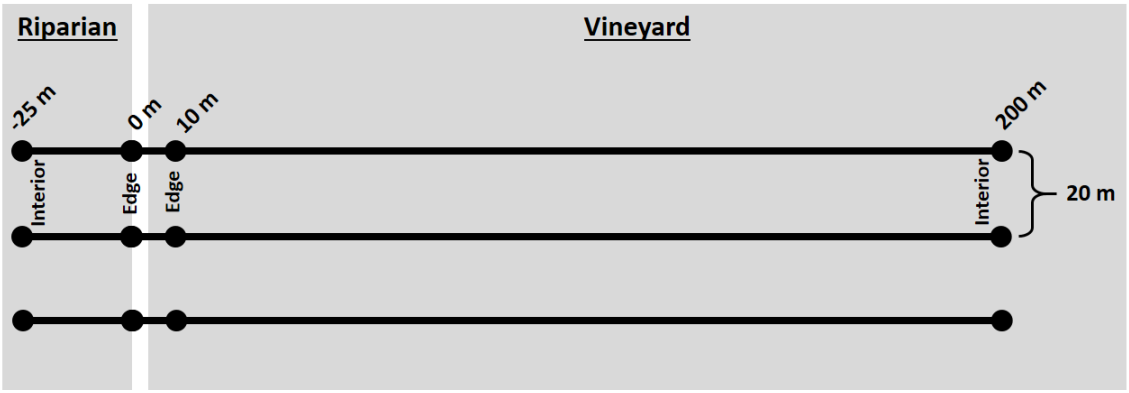
Field sites consisted of vineyard blocks >0.8 hectares (2 acres) adjacent to riparian habitat along the Russian River in Sonoma County, California, USA. There were 3 study sites in 2010, 5 sites in 2011 and 3 sites for follow-up work in 2013. All vineyard blocks were located on level ground with similar trellis and irrigation systems, and all were planted with red wine grape varieties (e.g., Cabernet sauvignon, Merlot etc.) that were at least five years old. All plots were maintained insecticide free throughout the course of the study, although the plots did receive sulfur applications to control fungi (and sulfur does have insecticidal properties). The riparian habitats typically included white alder (*Alnus rhombifolia* Nutt.), California laural (*Umbellularia californica* [Hook & Arn.] Nutt.), poplar (*Populus* sp.), California buckeye (*Aesculus californica* [Spach] Nutt.), willows (*Salix* spp.), Himalayan blackberry (*Rubus armeniacus* Focke), wild grape (*Vitis californica* Benth.) and, to a lesser extent, coyotebrush (*Baccharis pilularis* DC.), California walnut (*Juglans*

californica S. Watson), coast live oak (*Quercus agrifolia* Née), poison hemlock (*Conium maculatum* L.), and periwinkle (*Vinca major* L.).

Transects for sampling

At each site pests and natural enemies were sampled along three parallel transects (positioned 20 m apart) that extended out from the riparian habitat into the vineyard. Each transect was 225 m long: 25 m into the riparian habitat and 200 m into the vineyard. Along each transect samples were taken at the interior and edge of the riparian habitat (25 m and 0 m into the riparian habitat, respectively) as well as at the edge and interior of the vineyard (10 m and 200 m into the vineyard; see Figure 3.1). Vineyard interior samples were located at 200 m because continuous vineyard blocks rarely extended beyond this distance. Riparian interior samples were located 25 m from the edge because this is typically the maximum extent available before encountering a creek or river.

Figure 3.1 Riparian and vineyard transect sample point locations



Natural enemy and *Erythroneura elegantula* adult density

Between 15 April and 15 October (2010 and 2011) yellow sticky-traps were used to monitor *Anagrus* wasps and generalist predators as well as *E. elegantula* adults. At each of the four points (-25, 0, 10, 200 m) along each transect, a 16 x 10 cm yellow sticky-trap (Seabright Laboratories, Emeryville, CA) was hung from a metal pole at 1.8 m above ground level, placing the trap at or just above the upper vine canopy. Following Hogg and Daane (2010), traps were positioned so that only the sticky side of the trap faced the riparian habitat. Traps were replaced approximately every two weeks (total of nine sets of 2-week samples per year; 7 April – 8 October 2010 and 14 April – 13 October 2011).

Spider abundance in the vine canopy

In August or September of each year, spiders were sampled from the vine canopy using a modified beat-sheet following Costello and Daane (1997). The beat-sheet consisted of a 1 m^2 cloth funnel that fed into a detachable 3.78 liter (1 gallon) plastic bag. Five samples were each collected from randomly selected vines at both the vineyard edge and interior. Sampling involved holding the funnel beneath the grape vine canopy and vigorously shaking the vine for 30 seconds in order to dislodge spiders. All spiders were identified to family.

***Erythroneura elegantula* nymphs**

Leafhopper nymph populations were monitored approximately once per week from 15 April to 15 October in 2010 and 2011 and from 15 April to 15 June in 2013. Monitoring only took place at the vineyard edge and interior, as *E. elegantula* nymphs are restricted to grape vines. On each sample date at each site, 60 leaves were sampled from randomly selected vines at the vineyard edge and another 60 leaves from the vineyard interior. For the 1st generation of nymphs, leaves were sampled from shoot nodes 1-3; for the 2nd generation, leaves were sampled from shoot nodes 4-6, as this generation of leafhoppers oviposit onto new vine growth (Daane et al. 2013). Each leaf was inspected on both sides for leafhopper nymphs and the total number of nymphs was recorded for each sampled leaf.

Parasitism rates of leafhopper eggs

In a similar fashion, leafhopper egg parasitism rates were evaluated by collecting 30 leaves from randomly selected vines at both the vineyard edge and interior from each site. Parasitism rates were assessed twice each season in 2010 and 2011, once following peak nymph density of the 1st generation (1 - 15 June) and again following the peak of 2nd generation leafhopper nymphs (20 July – 15 August). In 2013 parasitism rates were evaluated only once, following peak 1st generation nymph density (1 - 15 June). Leaves were collected from shoot nodes 1 - 3 for the 1st generation and nodes 4 - 6 for the 2nd generation. Leaves were brought to the laboratory and inspected while viewed with a dissecting stereo microscope. Egg status was determined by the emergence mark present – a small slit in the egg close to the leaf surface indicated that a grape leafhopper had successfully emerged while a circular hole on the top of the egg indicated emergence of *Anagrus* (*Trichogramma* sp. and *Ufens* sp. can leave a similar emergence hole, but were not recovered during this study, Wilson unpublished data). Unemerged eggs were not included in the parasitism assessment, as their status could not be consistently determined.

Vine vigor

In 2013, grape vine total petiole percentage nitrogen content at peak bloom was quantified at each site. Peak bloom was defined as >80% of grape clusters in full bloom. Petioles were collected from 60 randomly selected vines at both the vineyard edge and interior. Following Reisenauer (1978), each petiole was taken from opposite flower clusters near the base of a shoot. A single petiole was collected from any given vine. Petioles were brought to the laboratory, where they were washed with deionized water, dried at 55°C for 24 hours, and then sent to the University of California Division of Agriculture and Natural Resources Analytical Laboratory for quantification of total nitrogen levels.

Statistics

Before analyses, data from all years of the study were pooled for analysis. To improve normality, all data on insect densities were log(x+1) transformed and all proportional data were arc-sine square root transformed. All data were analyzed with the statistics program R (version 3.0.3, *http://www.r-project.org/*).

Measurements taken at the vineyard edge and interior were assessed using two-tailed paired t-tests. This includes peak 1st and 2nd generation leafhopper adult and nymph density, leafhopper oviposition and egg-parasitism rates, canopy spider abundance and petiole total nitrogen levels. Measurements of "peak density" for each leafhopper generation occurred on one specific sample date for each vineyard and sample year and were averaged across the three transects at each site, resulting in one measurement per transect point per site. Oviposition and parasitism rates were also averaged across the three transects at each site.

Natural enemy density on yellow sticky-traps was compared among the four transect points using Analysis of Variance (ANOVA). Analyses were conducted for both early-season and seasonal measurements. Natural enemy densities were used as the dependent variable, and transect sample points were used as the independent variable. When ANOVA indicated a significant effect, Tukey's HSD test was used to determine differences between the transect points.

For each sample date, yellow sticky-trap data were averaged across each replicate's transect points at each site, resulting in one measurement per transect point per site per sample date. Natural enemy density was averaged across the first three sample dates in each year to determine early-season density (7 April – 23 June 2010 and 14 April – 30 June 2011). The same data were averaged across all sample dates in each year to determine seasonal density. Generalist predator diversity was quantified using the Shannon-Weiner diversity index.

RESULTS

Peak activity of *E. elegantula* adult density was not significantly different between edge and interior vines (1st generation $t_7 = -0.25$, $p = 0.81$; 2nd generation $t_7 = -1.24$, $p = 0.26$; 3rd generation $t_7 = -1.06$, $p = 0.33$; Figure 3.2). Leafhopper egg deposition rates were significantly lower on edge vines compared to interior vines for both generations (1st generation $t_8 = -4.7$, $p = 0.002$; 2nd generation $t_5 = -3.14$, $p = 0.03$; Figure 3.3).

Egg parasitism rates were not significantly different for both 1st generation ($t_5 = 1.2$, $p = 0.28$) and 2nd generation ($t_4 = -0.62$, $p = 0.57$) (Figure 3.4). Peak 1st generation leafhopper nymph populations were significantly lower on the edge compared with interior vines ($t_8 = -5.7$, $p = 0.0005$), but there was no significant difference in peak 2nd generation nymph populations ($t_5 = -1.95$, $p = 0.11$) (Figure 3.5).

Grape leaf petiole nitrogen contents significantly differed between edge and interior vines in 2013 ($t_2 = -10.71$, $p = 0.009$; Figure 3.6).

Both early-season and seasonal density of soldier beetles (Coleoptera: Cantharidae) were higher at measurement points within the riparian habitat (Early-season: $F_{3,8} = 6.03$, $p=0.003$; Seasonal: $F_{3,8} = 6.03$, $p=0.003$; Figure 3.7). All other predator groups, as well as overall predator density and

diversity, did not significantly differ among transect measurement points for either time period (Figure 8).

There was no significant difference in spider abundance (t_6=1.18, p=0.28), richness (t_6=0.36, p=0.73) or diversity (t_6 = 1.64, p = 0.15) between the vineyard edge and interior (Figure 3.9).

Early-season *Anagrus* wasp density did not significantly differ among transect measurement points ($F_{3,28}$=1.97, p=0.14), but seasonal density was significantly higher at the vineyard interior ($F_{3,28}$=4.17, p=0.02) (Figure 3.10).

Results from the follow-up sampling in 2013 mirrored observations from the 2010-2011 study. Once again lower *E. elegantula* egg deposition and nymph abundance were observed on vines closer to the riparian habitat but this was not matched with a similar trend in egg-parasitism by *Anagrus* wasps (Figure 3.11). Yet this time analysis of grape vine total petiole nitrogen content indicated significantly higher vigor of vines at the vineyard interior (Figure 3.6).

Linear regression did not indicate any absolute relationship between petiole nitrogen content and *E. elegantula* egg deposition across all of the sites in 2013, but when data was separated by individual site there appeared to be a strong correlation (though not significant, see Figure 3.12).

Figure 3.2 Peak *Erythroneura elegantula* adult density did not differ between the vineyard edge and interior for the first, second or third generation.

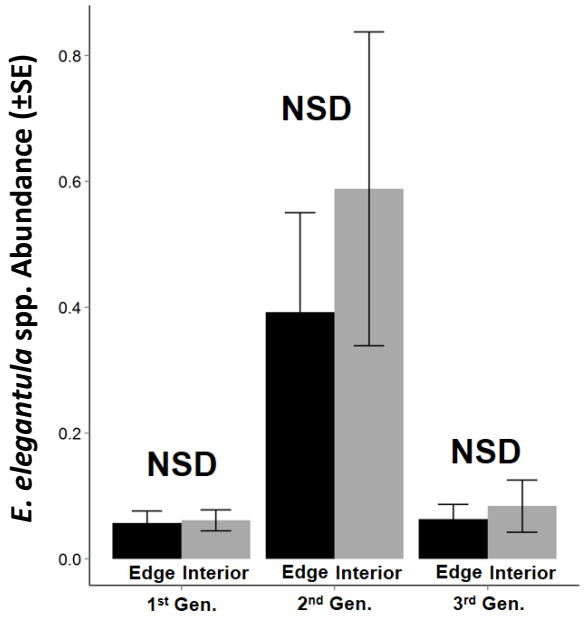


Figure 3.3 *Erythroneura elegantula* egg deposition was higher at the vineyard interior for both the first and second generation.

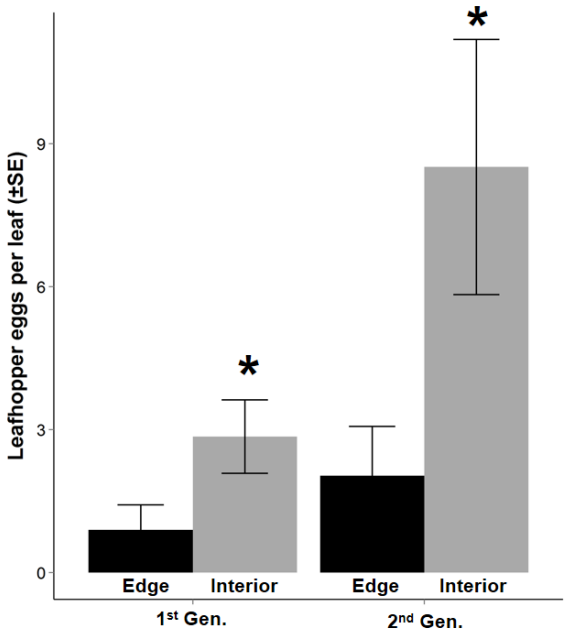


Figure 3.4 Parasitism of *Erythroneura elegantula* eggs did not differ between the vineyard edge and interior for either the first or second generation.

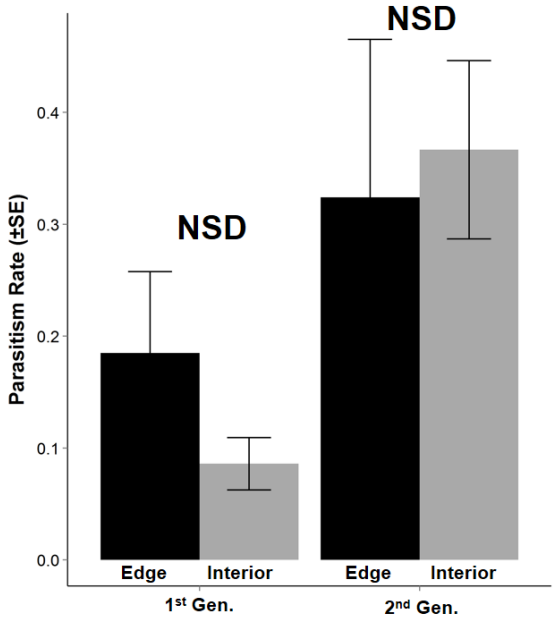


Figure 3.5 Peak *Erythroneura elegantula* nymph abundance was higher at the vineyard interior for the first generation, but not the second generation.

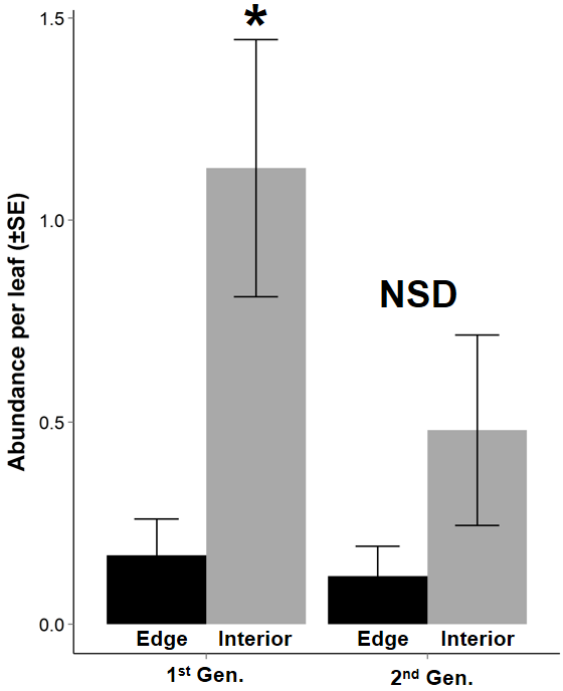


Figure 3.6 Difference in total percentage petiole nitrogen content between edge and interior vines averaged across all sites (3.6a) and paired by site (3.6b).

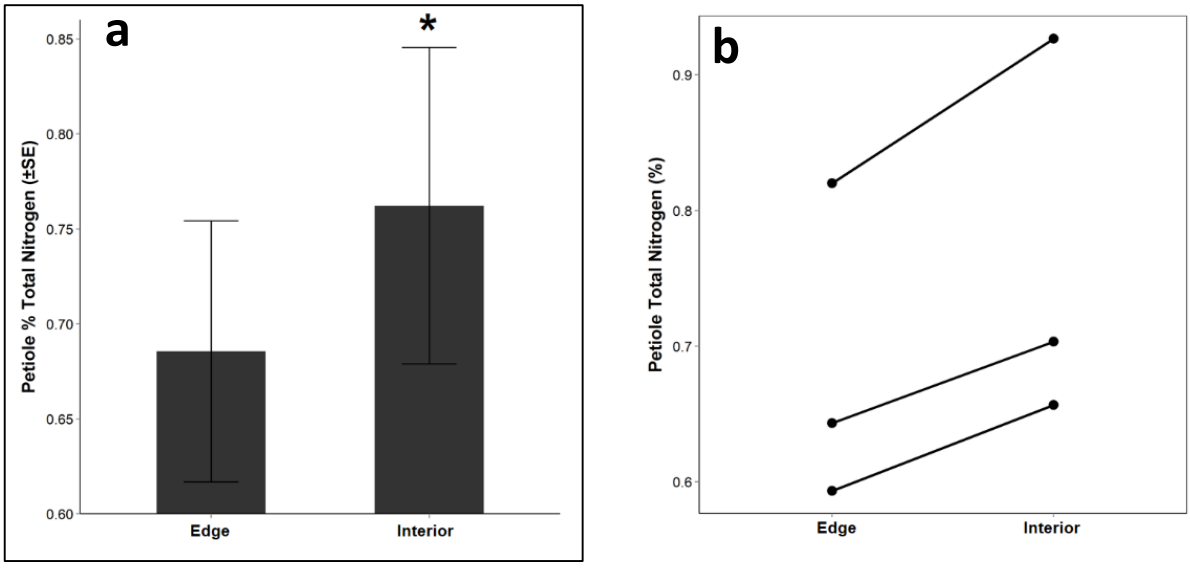


Figure 3.7 Cantharidae density over the entire season (3.7a) and by week (3.7b).

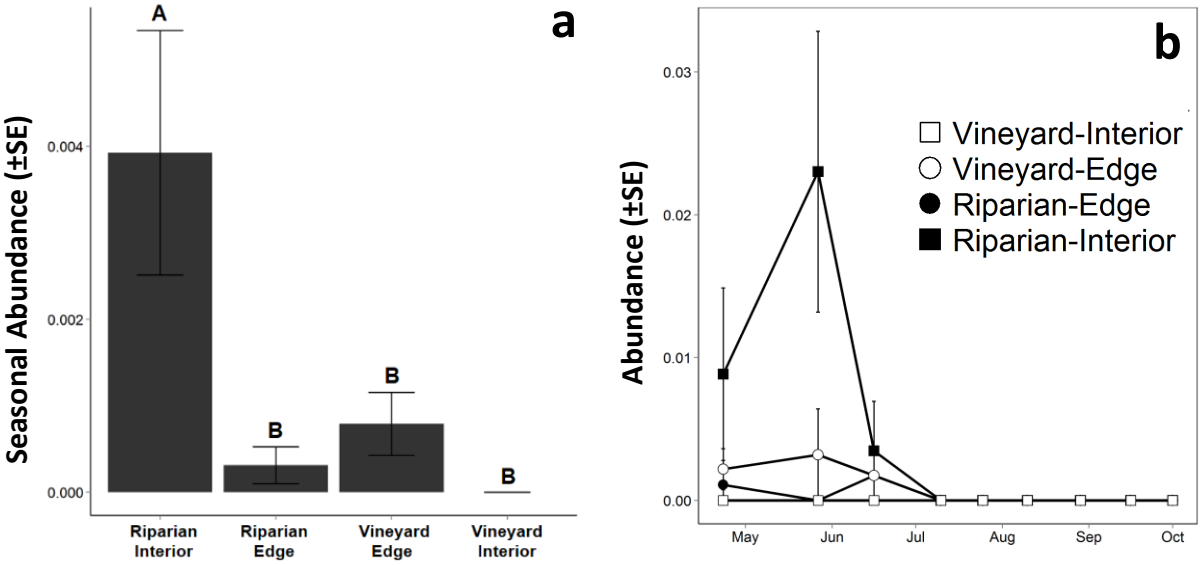


Figure 3.8 Generalist predator density in early-season (3.8a) and seasonal (3.8b)

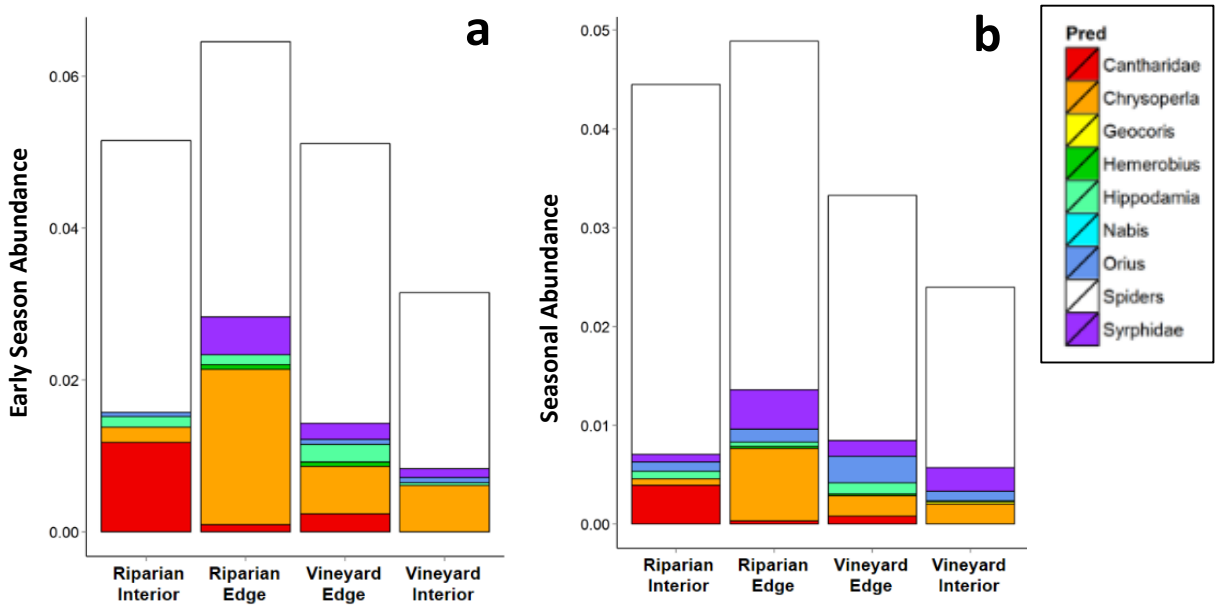


Figure 3.9 Spider abundance and species composition in the vine canopy did not differ between the vineyard edge and interior.

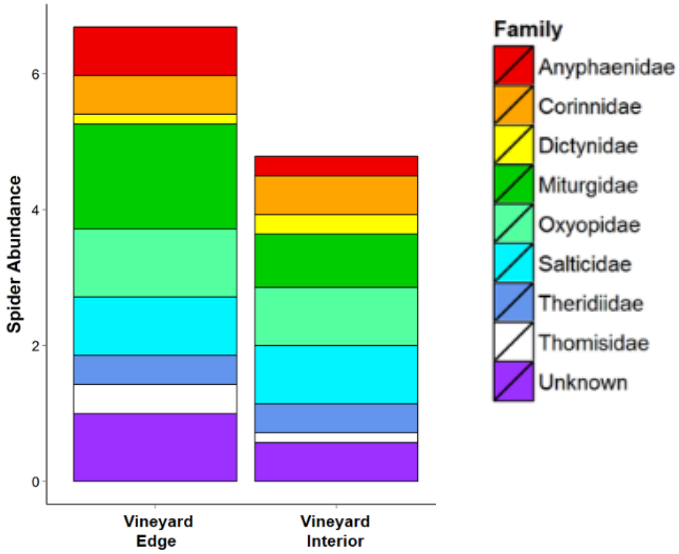


Figure 3.10. Density of *Erythroneura elegantula* (3.10a) and *Anagrus* spp. (3.10b) over the course of the growing season

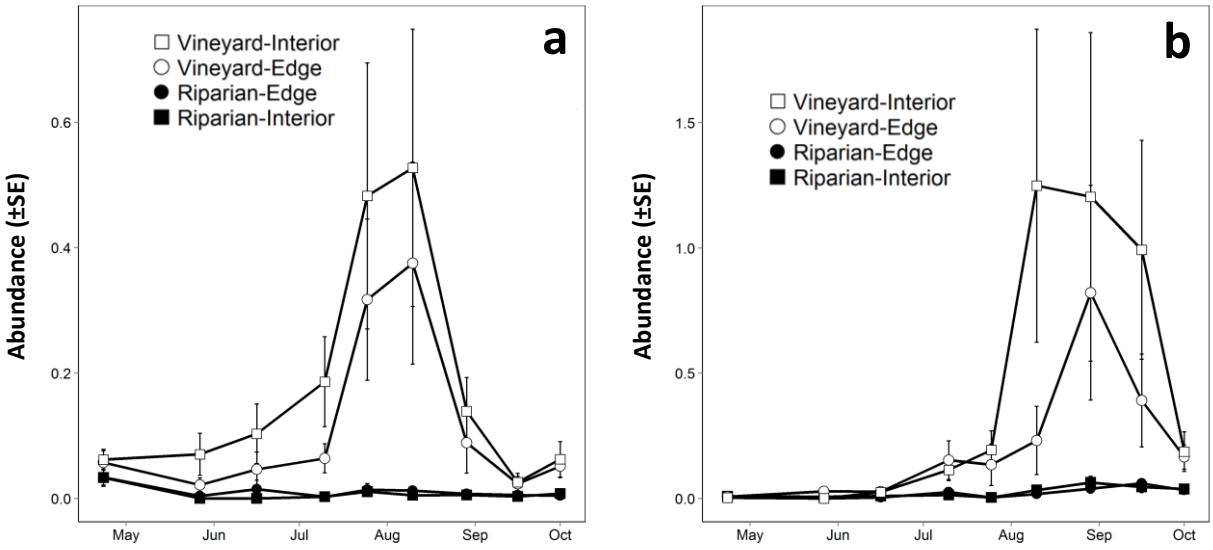


Figure 3.11 *Erythroneura elegantula* egg deposition (3.11a), parasitism rates (3.11b) and nymph abundance (3.11c) in 2013.

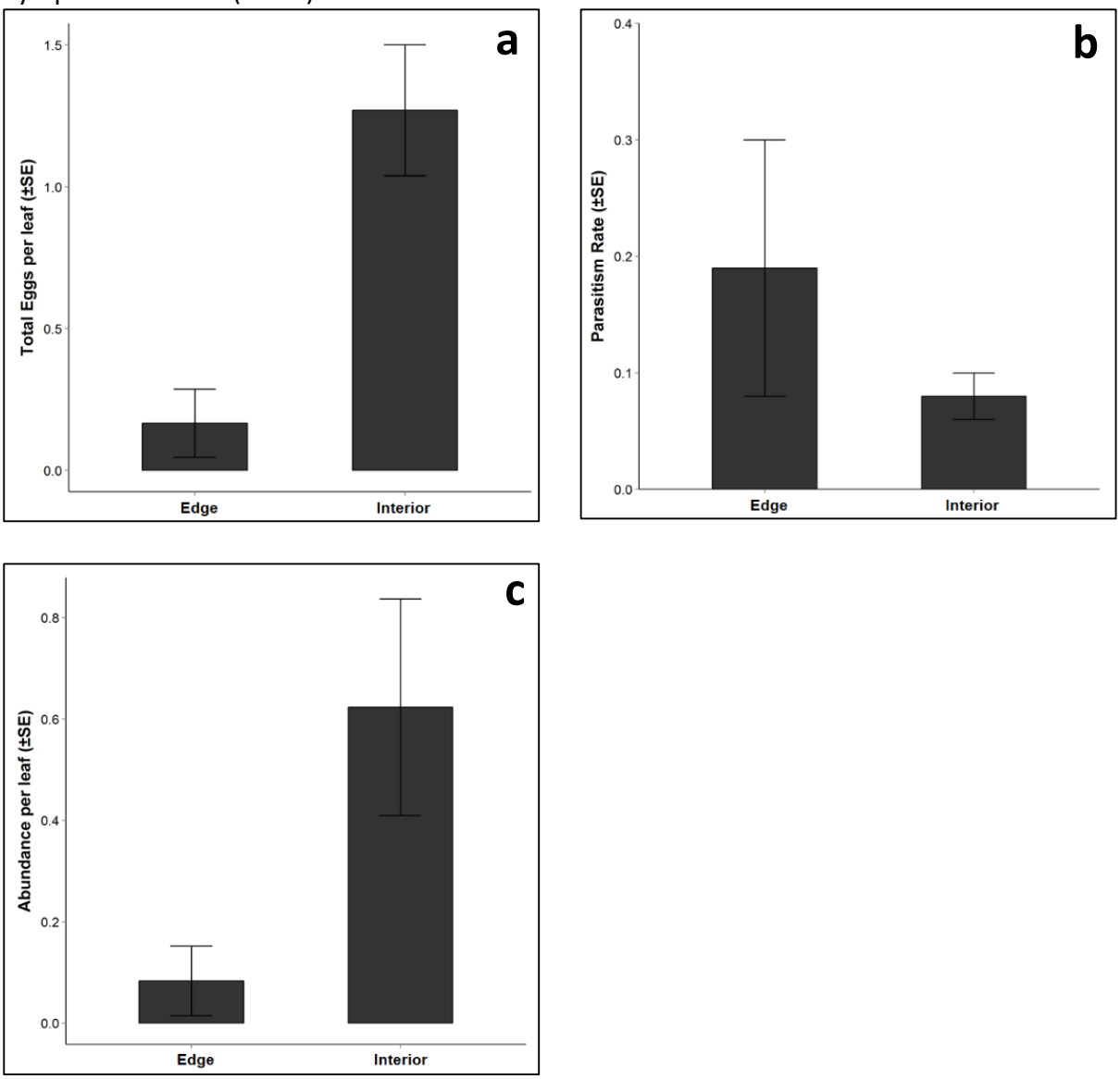
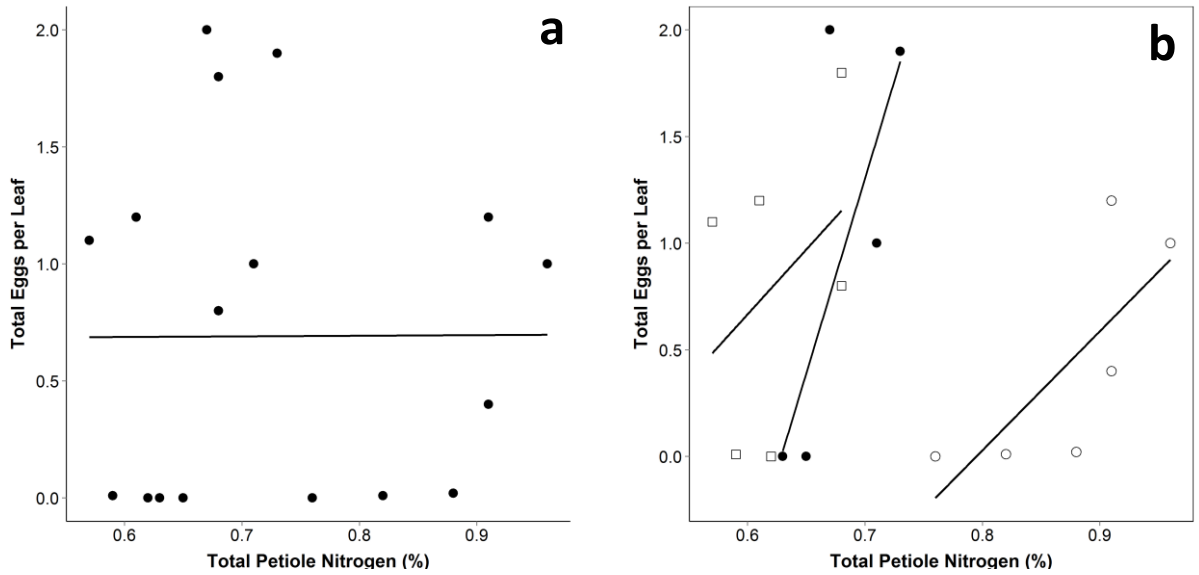


Figure 3.12 Relationship between total percentage petiole nitrogen content and *Erythroneura elegantula* egg deposition in 2013. All sites combined (3.12a); Grouped by site (3.12b).



DISCUSSION

Natural habitat intermixed with agroecosystems can increase biodiversity by reducing habitat fragmentation and has been advanced as a tool to improve ecosystem service provisioning to agriculture, particularly the biological control of pests (Thomas et al. 1991, Landis et al. 2000, Tscharntke et al. 2005, Bianchi et al. 2006). Here, this hypothesis was tested in vineyard ecosystems that abutted natural riparian zones by quantifying seasonal levels of a key leafhopper pest and its natural enemy complex. Results from two years study in multiple North Coast vineyards showed that vineyard population density of *E. elegantula* adults did not vary with distance away from the riparian habitat (Figure 3.2). The results did not, however, present a consistent pattern across all measured parameters, indicating the complexity of working at the landscape level to manipulate ecosystem services. For example, whereas leafhopper adult populations did not vary across the sampled transects, per leaf measurements of *E. elegantula* egg density (Figure 3.3) and subsequent nymph populations (Figure 3.5) were lower at the vineyard edge near the natural riparian zone. That vineyard leafhopper egg and nymph densities were lower near the natural habitat supports work by Nicholls et al. (2001) that found lower *E. elegantula* nymph populations near a riparian-woodland border. In this current study, the leafhopper density was low (<1.2 nymphs per leaf) and never exceeded the suggested economic injury level of 15 nymphs per leaf for wine grapes (Daane et al. 2013) and, for this reason, provides a forum to discuss causal mechanisms for observed leafhopper reductions rather than guidelines for management practices.

Previously, researchers have reported higher numbers of generalist predators on vines closer to riparian or wooded natural habitats, particularly spiders (Hogg and Daane 2010, 2011) and minute pirate bugs (*Orius* spp.) (Nicholls et al. 2001). An even greater number of studies have associated *Anagrus* spp. in vineyards with the proximity to riparian or wooded natural habitats (Doutt and Nakata 1973, Williams and Martinson 2000, English-Loeb et al. 2003, Ponti et al. 2005). In this current study, natural enemy density and *E. elegantula* egg parasitism rates did not follow similar spatial trends (Figures 3.4, 3.7, 3.8 and 3.9). The one exception to this was soldier beetles (Cantharidae), which exhibited higher density within the riparian habitat (Figure 3.6), but this never translated into higher densities within the vine canopy itself. Moreover, soldier beetles, like minute pirate bugs are not typically considered effective or key leafhopper predators. Higher *Anagrus* wasp populations at the vineyard interior were most likely the result of a density dependent response to increased *E. elegantula* populations in this area of the vineyard (Figure 3.10).

In the absence of any natural enemy impact, decreased *E. elegantula* populations at the vineyard edge appear to be related to decreased egg deposition rates (Figures 3.3 and 3.11), which could possibly be related to vine vigor. It is known that herbivorous insects are sensitive in a variety of ways to host-plant quality, in particular water stress and nutrient content (White 1974, Price 1991, Waring and Cobb 1992, Awmack and Leather 2002). The plant stress hypothesis predicts that induced water stress causes physiological changes in plants that leads to increased available nitrogen that, in turn, results in positive impacts on the survival and growth rates of insect herbivores feeding on these plants (Mattson 1980, White 1984, Mattson and Haack 1987). Key to this was the understanding that insects are N-limited (McNeil and Southwood 1978) and have thus evolved various mechanisms to cope with this limitation, including a preference for plants with elevated nitrogen levels (Mattson 1980). Subsequent work on this topic has shown that insect herbivores respond to plant stress in a variety of manners which has led to multiple revisions of the original hypothesis (Larsson 1989) as well as the introduction of complimentary theories, such as the plant vigor hypothesis (Price 1991). The plant vigor hypothesis states that younger plants with increased growth rates tend to experience more herbivory, possibly due to increased nutrient levels in developing plant tissue paired with a decrease in defensive chemical compounds (Price 1991). While the causation differs, elevated nutrient levels remain the key mechanism to explain improved herbivore performance on more vigorous plants. Other authors have logically extended the plant stress/vigor hypotheses to explain the relationship between soil fertility management, plant health and biological control of pests (Altieri and Nicholls 2003). The general idea is that the increased solubility of synthetic fertilizers (as versus compost or slow-release fertilizer) significantly elevates tissue nutrient levels and makes plants more preferable to herbivores. As with the other hypotheses, elevated nutrient levels is the key mechanism to explain herbivore response, in this case to soil fertility management. More recent meta-analyses have brought further attention to guild-specific responses to plant quality and indicate that sap feeders (and mesophyll feeders in particular, such as leafhoppers) appear to be more sensitive to changes in plant quality (Koricheva 1998, Huberty and Denno 2004). As such, it is no surprise that previous studies on leafhoppers have demonstrated a response to changes in plant water

stress (Hoffman and Hogg 1991, Leigh et al. 1974, Schowalter et al. 1999) and nutrient levels (Joerne et al. 2012, Iqbal et al. 2011, Richardson et al. 2002).

Similarly, in vineyards, *Erythroneura* leafhoppers have been shown to prefer vines with both higher nitrogen content (Mayse et al. 1991, Daane and Costello 1998) as well as irrigation levels (Trichilo et al. 1990, Daane and Williams 2003). More specifically, a number of these studies have shown increased *Erythroneura* egg deposition on vines with increased irrigation (Daane and Williams 2003) and nitrogen levels (Mayse et al. 1991).

These studies provided sufficient evidence to indicate that the changes in *E. elegantula* egg deposition observed in the 2010-2011 study may have possibly been related to changes in crop vigor and nutrient levels. As such, a sub-set of the original study sites was selected for follow-up sampling in 2013 in order to evaluate vine vigor as it related to *E. elegantula* egg deposition, nymph populations and parasitism rates. Grape vine total petiole nitrogen content was used as the metric of vine vigor.

Results from the follow-up sampling in 2013 mirrored observations from the 2010-2011 study. Once again lower *E. elegantula* egg deposition and nymph abundance were observed on vines closer to the riparian habitat but this was not matched with a similar trend in egg-parasitism by *Anagrus* wasps (Figure 3.11). Yet this time analysis of grape vine total petiole nitrogen content indicated significantly higher vigor of vines at the vineyard interior (see Figure 3.6).

Linear regression did not indicate any absolute relationship between petiole nitrogen content and *E. elegantula* egg deposition across all of the sites in 2013, but when data was separated by individual site there appeared to be a strong correlation (though not significant, see Figure 3.12). This indicates that *E. elegantula* may not have a static preference or threshold for total petiole nitrogen content but rather determine egg deposition sites based on relative differences in host-plant quality at a given site, a behavior which has been previously demonstrated for other herbivores (Bernays and Chapman 1994). Essentially *E. elegantula* is ovipositing into the best hosts possible given the limited selection at a specific vineyard site.

There is a large body of literature that explores the impacts of non-crop habitat adjacent to crop fields (such as windbreaks, hedgerows and field margins) on various crop development parameters, including nutrient levels and yield (see Kuemmel 2003, Marshall and Moon 2002 for reviews). Vineyard areas adjacent to riparian habitats could potentially have lower vigor due to changes in microclimate (Chen et al. 1995, 1999), increased plant competition (Nuberg 1998) and/or soil compaction due to farm machinery passing on dirt roads at the periphery of fields (Sparkes et al. 1998). In this study it appears that some combination of all 3 factors was likely at play, as all of the study sites had a dirt road running between the riparian edge and vineyard edge (see Figure 3.1) and woody perennial plants in the riparian habitats created a vegetation over-story that was at least 3-4 times greater than the height of grape vines, which resulted in significant shading of vines at the vineyard edge. While measures of petiole nitrogen content in 2013 obviously do not reflect crop condition in 2010-2011, vineyard management practices (and

soil fertility management in particular) remained the same in all years of this study and vine condition in 2013 did not appear to drastically vary from 2010-2011.

In a unique way the findings from this study validate 2 separate hypotheses: (1) that plant/stress vigor can influence insect herbivore host selection and (2) that proximity to patches of natural habitat can influence pest populations (White 1974, Mattson 1980, Price 1991, Tscharntke et al. 2005). Future studies on edge effects and biological control in fragmented landscapes would benefit by including measures of crop vigor in addition to data on invertebrate activity and natural enemy impact. Detailed information on the relationship between habitat diversity, crop vigor, pest populations and crop yield/quality would serve farm managers and policy-makers alike. At present there are a number of agri-environmental schemes (AES) in both the United States and Europe to support on-farm habitat diversification (hedgerows, windbreaks, cover crops etc.) to enhance a variety of ecosystem services, including biological control. While much has been written about the need to adjust these AES policies to account for landscape context (Kleijn et al. 2008, Concepcion et al. 2012), less frequently has it been argued that the on-farm practices themselves be adjusted to account for the variety of ecological mechanisms that may be at play. For example, hedgerows are typically promoted for their ability to attract and support natural enemies and enhance biological control of crop pests (Dufour 2000, Landis et al. 2000, Earnshaw 2004, Fiedler et al. 2008, Griffiths et al. 2008). The most commonly cited ecological mechanism for this predicted outcome is the natural enemies and/or resource concentration hypotheses (Root 1973, Letourneau 1987, Russell 1989, Andow 1991). Rarely is the role of crop vigor mentioned in this context, although it can be a key factor driving pest populations as demonstrated here. Ultimately growers interested in maintaining patches of natural habitat in and around their farms will need to reconcile the tradeoffs between biodiversity conservation, crop vigor management, biological control of pests and crop yield and quality.

Chapter 4: Changes in landscape diversity influence pests, but not natural enemies, in vineyard monocultures

ABSTRACT

Increasing the extent of crop production within an agricultural region can lead to the fragmentation and loss of natural habitats at a landscape scale. Studies have shown that reductions in the area and quality of these habitats surrounding crop fields can lead to a loss of key ecosystem services to agriculture, including biological control of pests. Due to perceived linkages between wine grape quality and geographic region, vineyard expansion at the expense of natural habitats is especially likely to occur within well-defined areas, such as California's popular North Coast wine grape growing region. This study evaluated how changes in the proportional area of natural habitat surrounding a vineyard (i.e., landscape diversity) influenced biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn) in Napa and Sonoma County vineyards. Over four years, data were collected on natural enemy and pest densities and pest parasitism rates from multiple vineyards that were situated in landscapes with low, intermediate and high levels of habitat diversity. Results from the study showed that while natural enemy densities and impact did not strongly respond to changes in landscape diversity, early season *E. elegantula* populations did appear to be lower in more diverse landscapes and this was thought to be related to increased predation of overwintering adults. These findings highlight how natural enemy dispersal capacity can mediate the effects of reduced landscape diversity as well as the importance of considering factors that contribute to biological control of pests outside of the growing season.

INTRODUCTION

On a global scale, the development and expansion of agriculture is the leading driver of natural habitat loss and associated biodiversity declines (Foley et al. 2005, Tilman et al. 2001, Sala et al. 2005). As biodiversity decreases so does ecosystem function (Hooper et al. 2005) and in particular ecosystem service provisioning to agriculture (Tscharntke et al. 2005). A number of studies have determined that an increase in the proportion of natural habitat surrounding an agroecosystem (i.e., increased landscape diversity) frequently correlates with increased ecosystem service provisioning to agriculture, including such important services as crop pollination (Ricketts et al. 2008) and biological control of arthropod pests (Bianchi et al. 2006).

The relationship between biological control and landscape diversity is usually attributed to the fact that agricultural regions that contain a wider variety of habitat types will have a greater probability of including important alternative resources that support natural enemies of crop pests, such as shelter, nectar and pollen, alternate hosts for parasitoids and prey for predators, and/or overwintering habitat in proximity to crop fields (Landis et al. 2000). Of course, the relationship between landscape-scale habitat diversity and ecosystem service provisioning to agriculture is not strictly linear and organismal response to changes in the landscape will likely vary according to life-history traits and habitat requirements as well as the quality and composition of natural and semi-natural habitats (Tscharntke and Brandl 2004). Although rare and contingent upon the botanical composition of natural habitats, in some cases it may even be that some diverse landscapes actually harbor overwintering pests that can lead to increases in crop loss that are not dampened by available ecosystem services. For instance, Roschewitz et al. (2005) found that aphid densities were higher in cereal crops located in more diverse landscapes, which was thought to be related to greater availability of aphid overwintering sites in the natural habitats.

Wine grape production in California is characterized by monoculture and specialized production, particularly in the San Joaquin valley. Wine grapes are a unique crop in that they are also subject to geographic branding (i.e., “terroir”) which provides additional incentive to replace natural habitats with expansive vineyard development in key wine grape growing regions, such California’s North Coast and, within it, Napa County and Sonoma County in particular (Heaton and Merenlender 2000).

Previous studies evaluating the relationship between landscape context and natural enemy response in vineyards are limited in number and have produced mixed results. Thomson et al. (2010) measured the population response of a number of parasitoids and predators in relation to changes in the area of woody vegetation surrounding vineyards. Although some parasitoids responded positively to increased landscape diversity (Eulophidae) others exhibited a negative response (Mymaridae and Trichogrammitidae) and there was no clear response pattern for any of the generalist predators evaluated. Isaia et al. (2006) observed a differential spider response in relation to landscape context. When grouped by hunting strategy, abundance of ambush spiders and specialized predators correlated with increased landscape diversity while sheet-web

weavers demonstrated a negative response. In California, Hogg and Daane (2013) found that abundance of an exotic spider (*Cheiracanthium mildei*) was positively correlated with increased proportions of vineyard in the surrounding landscape. Native spider populations followed an opposite trend. Finally, results from D'Alberto et al. (2012) showed that vineyard spider abundance was marginally correlated with the presence of pastures immediately adjacent to the vineyard, but the influence of landscape context itself was inconsistent. In sum, these studies demonstrate that the influence of landscape context on arthropod populations in vineyards can vary and is likely contingent on the plant species composition of natural habitats and the herbivores associated with them.

The western grape leafhopper (*Erythroneura elegantula* Osborn [Hemiptera: Cicadellidae]) is a key pest of wine grapes in California's North Coast region. *Erythroneura elegantula* overwinter as adults in reproductive diapause in leaf litter and on weedy vegetation and perennial plants (e.g., citrus) in and around vineyards. As temperatures increase and photoperiod changes to more sunlight in spring the vines start producing new shoots; at this time adult leafhoppers move onto fully-expanded mature grape leaves where they begin to feed and reproduce. Feeding by *E. elegantula* causes leaf stippling and reduced photosynthetic potential which can negatively impact crop quality and yield. *E. elegantula* resides on the grape leaves throughout the entire grape growing season (April – October) and, in Northern California, will typically complete two generations before the adults re-enter reproductive diapause and move back into the leaf litter as grape vines senesce and begin to lose their leaves at the end of the growing season (Daane et al. 2013).

The key parasitoids of *E. elegantula* are *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn (Hymenoptera: Mymaridae). These wasps attack the eggs of *E. elegantula* and are commonly found in many vineyards throughout Northern California. A number of generalist predators are also known to attack *E. elegantula*, including beetles in the family Cantharidae, *Chrysoperla* spp., *Geocoris* sp., *Hemerobius* sp., *Hippodamia convergens* Guérin-Méneville, *Nabis* sp., *Orius* sp., Syprhidae larvae and spiders (Daane et al. 2013). Prior research has established that spiders are one of the most abundant generalist predators in vineyards (>90% of the community in some cases) and thus one of the only natural enemy groups, other than *Anagrus* spp., thought to be present in sufficient densities to regulate *Erythroneura* leafhoppers (Costello and Daane 1999, 2003). Additional studies have indicated that *Orius* spp. may also play a significant role in the control of leafhoppers and thrips in vineyards (Nicholls et al. 2000, 2001).

Key to the relationship between *E. elegantula* and *Anagrus* wasps are their different overwintering habitat requirements. While adults of *E. elegantula* can successfully overwinter in leaf litter and on weedy vegetation or green perennial plants in and around vineyards, the *Anagrus* wasps must seek out and parasitize an alternate leafhopper host species that overwinters in the egg stage in order to successfully overwinter. These alternate hosts are typically found in natural and semi-natural habitats located outside of vineyards (Triapitsyn 1998, Lowery et al. 2007). As such, there is seasonal movement of *Anagrus* wasps between cultivated wine grapes (where they attack *E. elegantula* from April - September) and natural habitats (where

they attack alternate hosts to overwinter from October - March). Thus the expansion of wine grape vineyards at the expense of natural habitats is especially problematic for *Anagrus* spp. since they rely on these alternate habitats outside of vineyards to successfully overwinter and biological control of *E. elegantula* may be particularly susceptible to changes in the proportion of natural habitat surrounding vineyards.

While a number of studies have evaluated the influence of adjacent patches of natural, semi-natural and planted habitat (e.g. prunes) on natural enemies and biological control in vineyards (Doutt and Nakata 1973, Murphy et al. 1996, Murphy et al. 1998a, Murphy et al. 1998b, Nicholls et al. 2001, Williams and Martinson 2000, English-Loeb et al. 2003), only a few have considered the role of landscape context (Thomson et al. 2010, Isaia et al. 2006, D'Alberto et al. 2012, Hogg and Daane 2013), and none have actually evaluated how context influences natural enemy impact on pests.

In this study, biological control of *E. elegantula* was monitored in 33 vineyards situated along a continuum of landscape diversity (low to high landscape diversity) over the course of 4 years (2010-2013). The goal of this study was to evaluate whether or not natural enemy populations and biological control of *E. elegantula* is influenced by changes in the proportion of natural habitat surrounding the vineyard.

METHODS

Study sites

Field sites consisted of vineyard blocks >0.4 hectares (1 acre) located in Napa and Sonoma County, California, USA. There were 21 sites in 2010, 25 sites in 2011, 17 sites in 2012, and 7 sites in 2013. The sites were situated along a continuum of landscape diversity (i.e., sites were situated in low, intermediate and high diversity landscapes) and in each year of the study there were sufficient sites to represent a wide range of landscape types (i.e., each year there were sites in low, intermediate and high diversity landscapes). All vineyard blocks were located on level ground and consisted of grape vines that were red varieties (i.e., Merlot, Cabernet Sauvignon, Pinot Noir etc.) that were at least five years old. Each vineyard block was typically comprised of 40-80 vine rows with 50-80 vines per row. All samples were taken from 5 vine rows in the middle of each experimental plot. Within each of the sample rows no measurements were taken from the first or last ten vines. All plots were maintained insecticide free throughout the course of the study with the exception of mandatory sprays that were part of an eradication program for the invasive European grapevine berry moth (Tortricidae: *Lobesia botrana* Denis & Schiffenmüller) in 2010-2012 (Varela et al. 2010). These sprays consisted of non-contact products with low natural enemy impacts, including insect growth regulators, diamides, microbial insecticides (e.g. *Bacillus thurigiensis*), avermectins and spinosyns. These pesticides are thought to have little or no impact on *E. elegantula* populations.

Natural enemy and *E. elegantula* adult abundance

Yellow sticky-traps were used to monitor the abundance of *Anagrus* wasps, key generalist predators and *E. elegantula* adults between 15 April and 15 October each year of the study. At each vineyard site, five yellow sticky-traps (16 x 10 cm; Seabright Laboratories, Emeryville, CA) were randomly assigned to vines within the sampling area and hung in the vine canopy from a trellis wire. Traps were replaced approximately every two weeks.

***Erythroneura elegantula* nymph abundance**

Leafhopper nymph abundance was monitored approximately once a week from 15 April to 15 October. On each sample date, 60 leaves were sampled from randomly selected vines at each site. For the 1st generation of nymphs, leaves were sampled from shoot nodes one to three. For the 2nd generation, leaves were sampled from shoot nodes four to six, as the later generation of leafhoppers oviposit onto the more recent shoot growth. Each leaf was inspected on both the top and bottom sides for leafhopper nymphs and the total number of nymphs per leaf was recorded.

Leafhopper egg parasitism rate

In a similar fashion, leafhopper egg parasitism rates were evaluated by collecting 30 leaves each from randomly selected vines at each site. Parasitism rates were assessed twice each season following peak nymph density of the 1st generation (~1-15 June) and 2nd generation (~20 July – 15 August). Leaves were collected from shoot nodes one to three for the 1st generation and nodes four to six for the 2nd generation. Leaves were brought to the laboratory and inspected with a dissecting microscope. Egg status was determined by the emergence mark present – a small slit in the egg close to the leaf surface indicates that a grape leafhopper had successfully emerged while 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 it was impossible to tell whether these eggs were healthy or parasitized.

Spiders in the vine canopy

In August or September, spiders were sampled from the vine canopy using a modified beat-sheet following Costello and Daane (1999). The beat-sheet consisted of a 1 m^2 cloth funnel that fed into a detachable plastic bag. Five samples were each collected from randomly selected vines at each vineyard site. Sampling involved holding the funnel beneath the grape vine canopy and vigorously shaking the vine for 30 seconds in order to dislodge spiders. All spiders were brought to the laboratory and identified to family.

Vine vigor

Petiole total nitrogen (%) at peak bloom was quantified to assess vine vigor in 2011, 2012 and 2013. Peak bloom was defined as >80% of grape clusters in full bloom. At peak bloom, petioles were collected from 60 randomly selected vines at each site. Following Reisenauer (1978), each petiole was taken from opposite flower clusters near the base of a shoot. Only one petiole was collected from any given vine. Petioles were brought to the laboratory, washed with deionized

water and dried at 55°C for 24 hours. Samples were then sent to the University of California Division of Agriculture and Natural Resources Analytical Laboratory and total nitrogen levels were determined.

Natural enemy-exclusion study

A natural enemy-exclusion experiment was conducted at a subset of the research sites in 2011, 2012 and 2013. There were nine sites in 2011, eight sites in 2012, and two sites in 2013. As with the larger study, this subset of vineyards represented a range of low, intermediate and high diversity landscape types. The goal of this sub-study was to evaluate how changes in landscape diversity influenced the impacts of natural enemy-exclusion.

In the early spring, prior to bud break, exclusion cages were placed over one spur on 10-15 randomly selected vines at each study site. Each cage consisted of a 3.8 liter paint-strainer bag that was held open by two wire hoops (20.3 cm diameter, 20 gauge wire). The hoops were secured with wire to the vine trellis in order to hold the cage upright and allow for normal shoot development inside. Cages were then sealed around the bottom of the spur using wire twist-ties.

Typically multiple shoots would develop from the spur that was isolated within the cage. As such, following bud break all but one shoot was removed from the cage. As shoot development continued, a small opening was made in the top of the cage to allow the shoot to continue growing beyond the confines of the cage. The small opening was sealed around the shoot with rubber bands. The result of this was that each cage contained three to five leaves (shoot nodes one to five).

In mid-June, cages were inoculated with 10-20 adult *E. elegantula* (1:1 M:F). The adults were allowed to oviposit onto the caged leaves for four weeks. Cages were then removed from half of the vines at each site, exposing the leaves with *E. elegantula* eggs to natural enemies in the vineyard. After four weeks of exposure, *E. elegantula* nymph abundance was recorded for leaves on the caged and exposed vines. These same leaves were then brought to the laboratory where *E. elegantula* egg parasitism was assessed.

Quantification of landscape diversity

Landscape diversity was quantified by extracting “rangeland cover type” from the CalVEG dataset (US Forest Service 2010) using ArcGIS 10.1 (ESRI, Redlands, USA). There were 71 possible values for rangeland cover type (see Shiflet 1994 for descriptions). The total area of each cover type was calculated within a 500 m radius around each vineyard site. Cover types were then consolidated into five categories: “natural”, “agriculture”, “development”, “water” and “no data”. The proportion of cover by each category type was then calculated for each vineyard.

Statistics

Data from the five yellow sticky-traps in each plot at each site was averaged for each two week sample period and then summed across the “early-season” and “mid-season” range of sample

dates (Table 4.1). The sum of these two data sets was then used to calculate "seasonal" abundance of pests and natural enemies on the sticky-traps.

Two separate analyses were conducted for "early-season" and "seasonal" data on natural enemies in order to determine whether or not changes in landscape diversity had any influence on natural enemy abundance in the experimental plots during these two periods. The "early-season" and "mid-season" sample periods for the yellow sticky-traps coincided with 1st and 2nd generation peak *E. elegantula* adult populations respectively. Peak 1st and 2nd generation *E. elegantula* nymph abundance was determined by examining weekly nymph counts and identifying populations peaks. First and second generation *E. elegantula* adult and nymph abundance were strongly correlated and thus analyses on adults and nymphs were essentially redundant. For this reason only *E. elegantula* adult abundance was analyzed here. Data from the beat samples of the vine canopy (Table 4.2) were summed for each plot at each site in each year of the study (T = one measure per plot per site per year for the canopy shake samples). Natural enemy diversity was quantified using the Shannon-Weaver index (H'): $H' = - \sum (P_i * \ln P_i)$ where P_i is the fraction of the entire population made up of species *i*. A high value of H' would represent a more diverse and equally distributed community. A value of zero would represent a community with only one species. All data were analyzed with the statistics program R (version 3.0.3, http://www.r-project.org/).

Table 4.1 Yellow sticky-trap sample dates

Period	Year	Sample Dates Range	Cumulative Number of Days
Early-Season	2010	29 April – 4 June	38
	2011	13 April – 25 May	42
	2012	24 April – 6 June	43
	2013	12 April – 22 May	41
Mid-Season	2010	6 July – 18 August	43
	2011	14 July – 7 September	54
	2012	10 July – 21 August	42
	2013	14 July – 28 August	45

Table 4.2 Spider sampling in the vine canopy

Year	Sample Date
2010	2 September
2011	11 August
2012	12 September
2013	15 September

Natural enemy and pest activity-density from the yellow sticky-traps, parasitism rates, spider populations from the canopy shake sampling, and crop vigor were each evaluated with generalized linear models (GLMs). Because most of the data in this study did not follow a normal distribution GLMs were used to allow for the specification of alternate error structures. As such,

a negative binomial distribution was used for all count data and a quasibinomial distribution was used for proportional data in order to adjust for both the non-normal distribution as well as overdispersion of the data (Zuur et al. 2007, Crawley 2012)

For each response variable, a full model was constructed that contained all possible explanatory variables and then likelihood ratio tests were used to evaluate the influence of individual explanatory variables via single term deletions ("drop1" command with X^2 tests [for negative binomial data] and F tests [for quasibinomial data] in package "lme4"). When data appeared normally distributed, a Gaussian (normal) error structure was used and single term deletion tests were evaluated with F tests. This is essentially the same as analysis of covariance. This type of analysis was used on all measures of total predator activity-density, richness and diversity from the yellow sticky-trap data, spider abundance, richness, and diversity from the canopy shake sampling, as well as on measures of crop vigor. All of the Gaussian and quasibinomial models were constructed using the "lme4" package and negative binomial models were constructed with the "MASS" package in R version 3.0.3.

All analyses of natural enemy populations included "proportion natural habitat within 0.5 km radius" as the key explanatory variable. Parasitism rates included "proportion natural habitat within 0.5 km radius", "*Anagrus* spp. abundance", and "*E. elegantula* abundance" as explanatory variables. Analyses of 1st generation *E. elegantula* adult abundance included "proportion natural habitat within 0.5 km radius", "grape variety", and "total petiole nitrogen (%)" as explanatory variables. Analyses of 2nd generation *E. elegantula* adult abundance included the additional explanatory variables "seasonal predator abundance", "canopy spider abundance", and "1st generation parasitism rate".

RESULTS

Seasonal natural enemy abundance

Seasonal *Anagrus* spp. abundance was not significantly influenced by landscape diversity (LRT = 2.5, p = 0.11), but rather strongly responded to *E. elegantula* abundance (LRT = 54.3, p = <0.001; Figure 4.1b).

Seasonal abundance of *Hippodamia convergens* was significantly increased in more diverse landscapes (LRT = 4.9, p = 0.03), but none of the other individual predator family/genera demonstrated significant response to changes in landscape diversity. Similarly, overall predator abundance, richness and diversity were not significantly influenced by landscape diversity (Abundance F = 4, p = 0.05; Richness LRT = 0, p = 0.98; Diversity LRT = 0.005, p = 0.95). Since *Hippodamia convergens* was not found on sticky traps after the "early-season" period, the correlation of "seasonal" abundance with landscape diversity is an artifact of "early-season" abundance.

Landscape diversity had no influence on overall spider abundance, richness or diversity in the vine canopy (Abundance LRT = 2.3, p = 0.13; Richness F = 1.1, p = 0.29; Diversity F = 0.07, p = 0.8). When evaluating individual spider families, it was found that abundance of Anyphaenidae was increased in vineyards situated in more diverse landscapes (LRT = 7.8, p = 0.005; Figure 3a).
Early season *Anagrus* spp. abundance was not significantly influenced by landscape diversity (LRT = 2.5, p = 0.11) but did respond to *E. elegantula* abundance (LRT = 54.3, p = <0.001; Figure 4.1a). Whereas early season activity of *Hippodamia convergens* was significantly influenced by landscape diversity (LRT = 4.9, p = 0.03; Figure 4.3b), none of the other individual predator family/genera had significant population responses to landscape diversity; similarly, overall early-season predator abundance, richness and diversity were also not significantly influenced by landscape diversity (Abundance LRT = 3.1, p = 0.08; Richness F = 0.007, p = 0.94; Diversity F = 0.13, p = 0.72). See Figure 4.2 for a summary of data on natural enemy activity-density in the crop canopy.

Figure 4.1 *Anagrus* spp. abundance correlates with *E. elegantula* abundance. Early season abundance (4.1a); Seasonal abundance (4.1b).

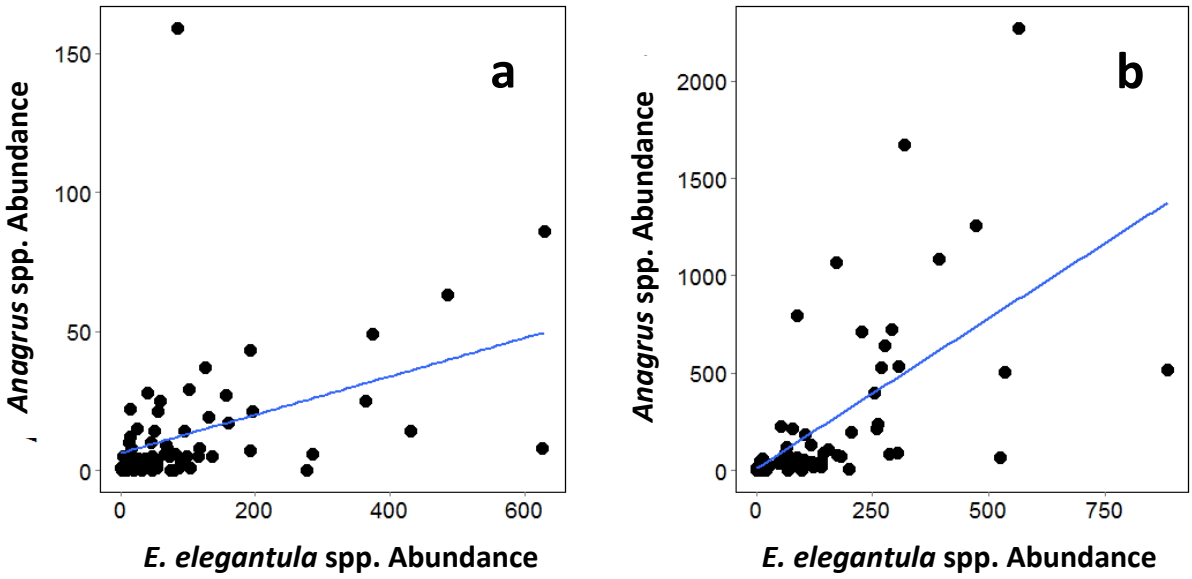


Figure 4.2 Natural enemy abundance in the vine canopy. Seasonal is the sum of early and mid-season densities.

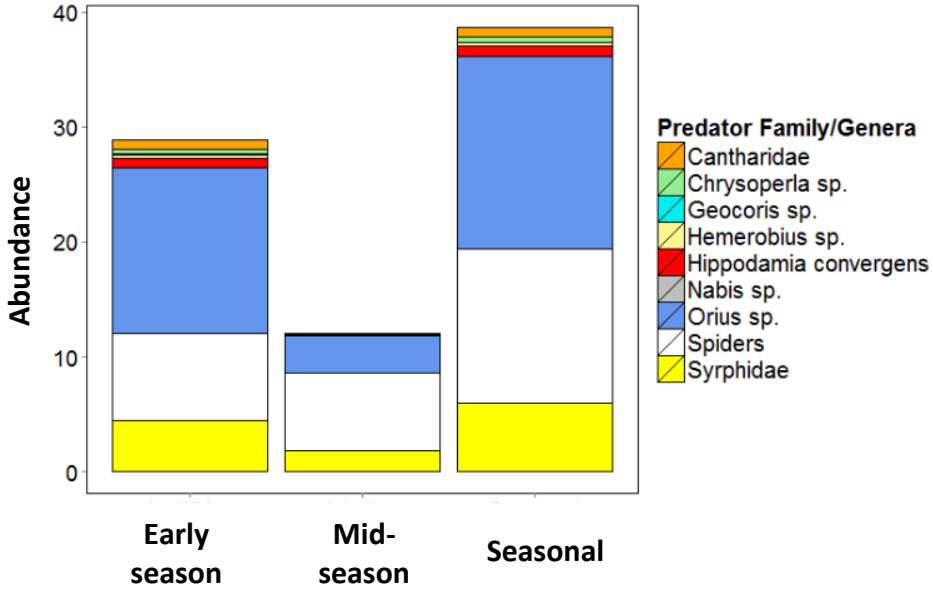
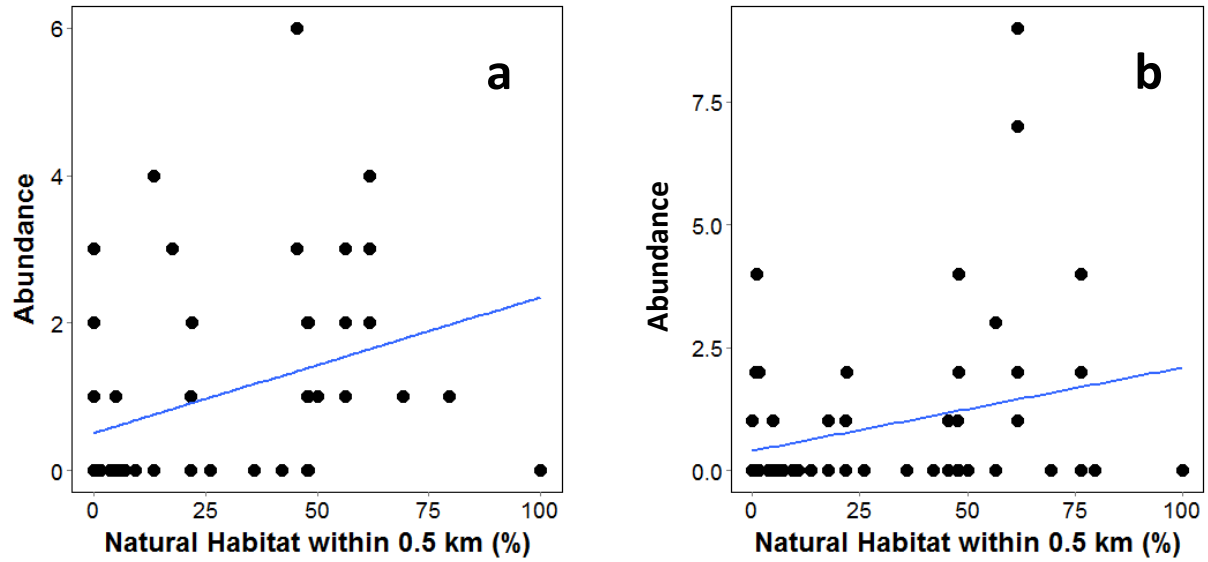


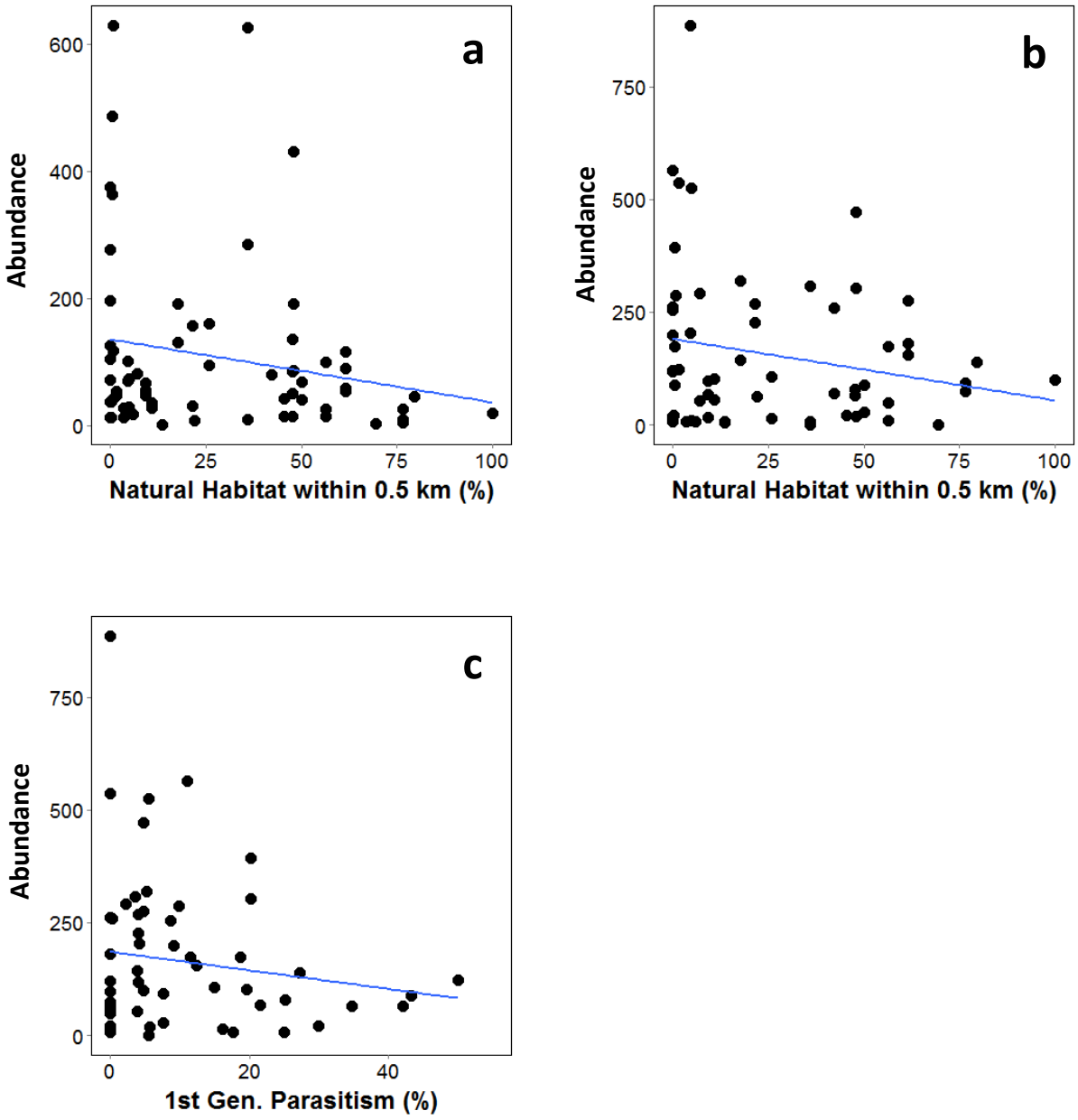
Figure 4.3 Abundance of some natural enemies increased in more diverse landscapes. Anyphaenidae in the vine canopy (4.3a); early-season *Hippodamia convergens* (4.3b).



First generation *E. elegantula* abundance was significantly lower in more diverse landscapes (LRT = 6.3, p = 0.01; Figure 4.4a) and was not influenced by grape variety (LRT = 4.4, p = 0.11) or petiole nitrogen content (LRT = 0.23, p = 0.63). Second generation *E. elegantula* abundance was not

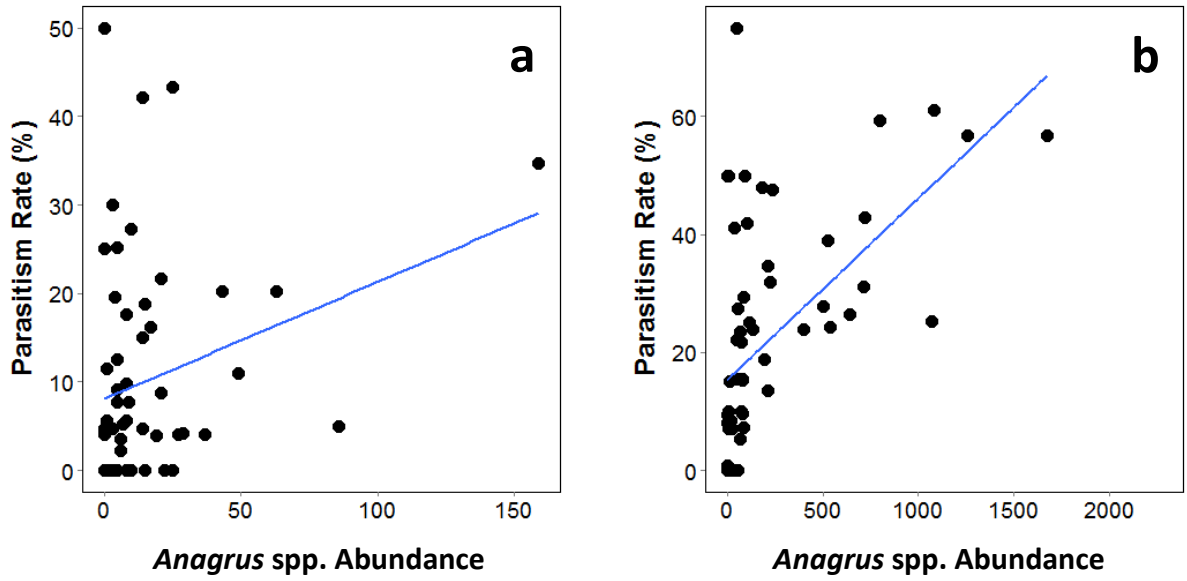
significantly influenced by landscape diversity (LRT = 2.3, p = 0.16; Figure 4.4b), grape variety (LRT = 0.34, p = 0.56), petiole nitrogen content (LRT = 0.01, p = 0.98), 1st generation parasitism rate (LRT = 0.42, p = 0.52; Figure 4.5), seasonal predator abundance (LRT = 0.65, p = 0.43), or spider abundance in the vine canopy (LRT = 0.33, p = 0.57).

Figure 4.4 Landscape diversity influenced first generation *E. elegantula* abundance (4.4a) but not second generation abundance (4.4b). First generation parasitism rates did not influence second generation *E. elegantula* abundance either (4.4c).



Parasitism of both 1st and 2nd generation *E. elegantula* eggs was significantly influenced by *Anagrus* spp. abundance (1st gen. F = 5.3, p = 0.03; 2nd gen F = 38.8, p = <0.001; Figures 4.5a and 4.5b) but not by landscape diversity (1st gen. F = 0.12, p = 0.73; 2nd gen. F = 1.4, p = 0.25) or *E. elegantula* activity (1st gen. F = 0.43, p = 0.51; 2nd gen. F = 0.37, p = 0.55).

Figure 4.5 Parasitism of first and second generation *E. elegantula* was positively correlated with *Anagrus* spp. abundance. First generation parasitism rates (4.5a); Second generation parasitism rates (4.5b).



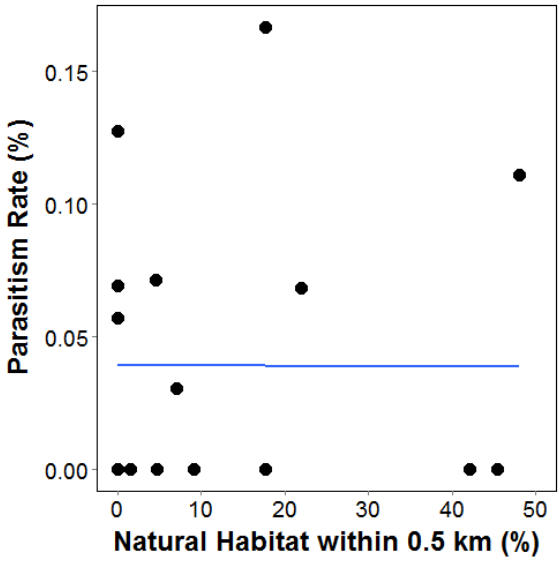
Natural enemy-exclusion study

In all years of the study the cage and false-cage treatments did not have any significant influence on temperature (2011 $F_{2,5} = 0.32$, p = 0.75; 2012 $F_{1,5} = 0.90$, p = 0.40; 2013 $F_{1,5} = 0.15$, p = 0.72) or relative humidity (2011 $F_{2,5} = 1.4$, p = 0.37; 2012 $F_{1,5} = 0.02$, p = 0.89; 2013 $F_{1,5} = 0.38$, p = 0.57). There were no significant differences between exposed and false-cage treatments in leafhopper egg deposition ($F_{1,17} = 0.71$, p = 0.41), parasitism rate ($F_{1,17} = 0.003$, p = 0.96) or nymph populations ($F_{1,17} = 0.17$, p = 0.68). These findings demonstrate that the cage itself had no influence on microclimate or *E. elegantula* population in the cages. As such, the "false cage" treatment was not used in subsequent experiments (2012 and 2013). There were no significant differences in leafhopper egg deposition between the different cage treatments ($F_{2,36} = 1.3$, p = 0.30) or between sites ($F_{12,34} = 1.9$, p = 0.10).

In 2011 the leaves from all caged vines were examined for parasitism in order to validate the effectiveness of the cages. There was no evident parasitism of any caged leaves in 2011 and thus

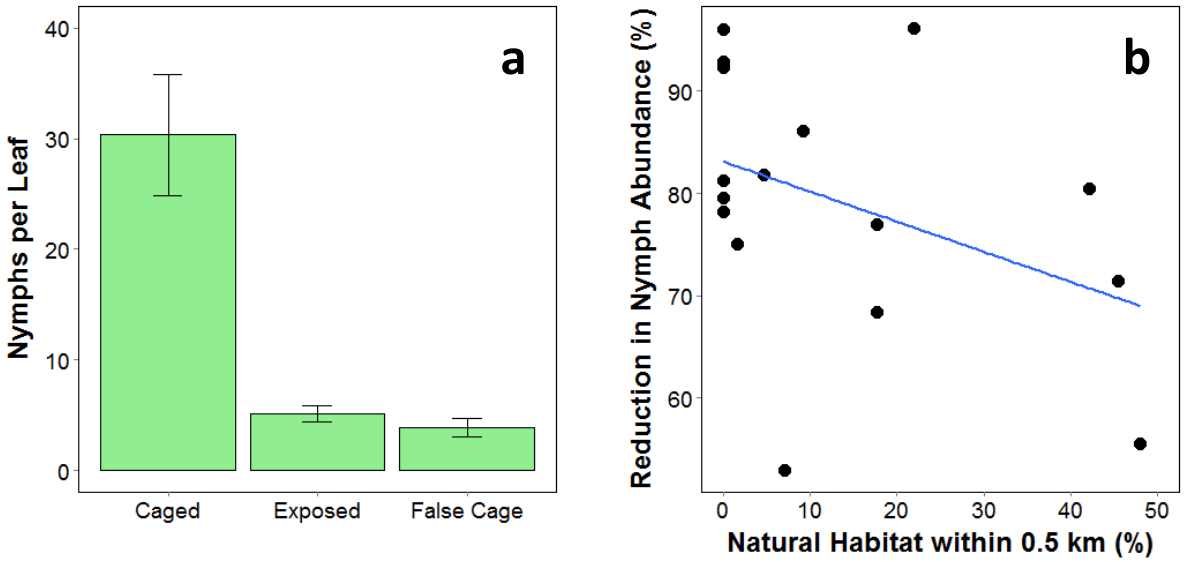
in subsequent studies (2012 and 2013) only data on *E. elegantula* nymph populations was recorded from leaves on the caged vines. Parasitism of sentinel *E. elegantula* eggs from the exposed vines was not significantly influenced by landscape diversity (LRT = 1.3, p = 0.26) or *Anagrus* spp. activity (LRT = 2.1, p = 0.15) (Figure 4.6).

Figure 4.6 Parasitism of *E. elegantula* eggs on exposed leaves



Caged vines did have significantly more *E. elegantula* nymphs than exposed vines ($F_{2,46}$ = 13.2, p = <0.001; Figure 4.7a), but the proportional reduction in nymph populations did not correspond with changes in landscape diversity (F = 0.71, p = 0.41; Figure 4.7b), parasitism rate of exposed leaves (F = 0.94, p = 0.35), seasonal predator abundance (F = 0.82, p = 0.38) or canopy spider abundance (F = 0.05, p = 0.83).

Figure 4.7 Results from the natural enemy-exclusion study. *E. elegantula* nymph abundance (±SEM) on caged, exposed and false-cage treatments (4.7a); Relationship between landscape diversity and percentage reduction in nymph abundance on exposed leaves (4.7b).



DISCUSSION

Leafhopper abundance appeared to be primarily determined by landscape diversity (i.e., the proportion of natural habitat within 0.5 km of the vineyard), rather than grape variety, crop vigor, parasitism rate, or natural enemy populations. Activity of *Anagrus* spp. did not correlate with changes in landscape diversity but rather closely matched activity of *E. elegantula* across all of the sites and parasitism rates of 1st and 2nd generation *E. elegantula* eggs was significantly influenced by *Anagrus* spp. activity. While this has positive implications for biological control of *E. elegantula*, it also showed that high parasitism rate of 1st generation leafhopper eggs did not consistently lead to reductions in 2nd generation *E. elegantula* adult activity. Generalist predators did not appear to consistently respond to changes in landscape diversity either, although *H. convergens* was in greater abundance in more diverse landscapes early in the season and abundance of spiders in the family Anyphaenidae were also positively correlated with increased landscape diversity. With regards to natural enemy population response, these findings match with Thomson et al. (2010) and D'Alberto et al. (2012), who both found weak and/or inconsistent natural enemy response to changes in landscape diversity. These findings are also similar to Isaia et al. (2006) in that not all groups of spiders responded in the same way to changes in landscape diversity.

Results from the natural enemy-exclusion study were inconclusive. Although natural enemy exclusion did result in significantly higher *E. elegantula* nymph populations, this was not

explained by natural enemy populations, parasitism rates or landscape context. It may have been that decreased nymph populations on the exposed vines were simply lower due to movement into other parts of the vine canopy, as this was not controlled for. Parasitism of sentinel leafhopper eggs on the exposed vines did not correlate with *Anagrus* spp. activity-density or landscape context either.

In the absence of significant effects related to natural enemy populations or parasitism rate, the relationship between *E. elegantula* abundance and landscape diversity may be related to survival of overwintering adults. As mentioned, *E. elegantula* overwinter as adults in leaf litter and low growing vegetation in and around vineyards from late October – early April. During this time they are likely subject to some degree of predation by ground predators and/or susceptible to entomopathogenic fungi due to cold/moist conditions.

While a majority of biological control studies focus on pest and natural enemy dynamics within the growing season, some studies have evaluated the survival of overwintering pest populations. Solomon et al. (1976) found that populations of overwintering codling moth (*Cydia pomonella* L., Lepidoptera: Tortricidae) in apple orchards were reduced by as much as 95% due to predation by avian predators. Similar studies also recorded high rates of avian predation on overwintering larva and pupa (MacLellan 1958, Le Roux 1959, Mailloux and Le Roux 1960). Glen and Milson (1978) found that in addition to avian predation, *C. pomonella* larvae overwintering on the ground were also less likely to survive in damp soil conditions and many were found to have been killed by a variety of fungi including *Verticillium lecani* (Zimm.) Viegas, *Mettarhizium anisopliae* (Metchnikoff) Sorokin, and *Fusarium* sp.

In almond orchards, Eilers and Klein (2009) observed that overwintering navel orangeworm (*Amyelois transitella* Walker, Lepidoptera: Pyralidae) were subject to both parasitism and vertebrate predation and that the impact of these natural enemies was increased in orchards situated in more diverse landscapes as well as orchards containing more diverse ground covers. Summers et al. (2004) noted that survival of overwintering corn leafhopper (*Dalbulus maidis* Delong & Wolcott, Hemiptera: Cicadellidae) in California was likely improved by an increase in the area and frequency of corn cultivation in the San Joaquin Valley in the mid-1990s. In effect, landscape simplification due to increased corn production improved and increased *D. maidis* overwintering habitat, which allowed it to permanently establish as a pest in this region.

With regards to leafhoppers on grape specifically, McKenzie and Beirne (1972) noted that winter cultivation of vineyards could reduce overwintering populations of the Virginia creeper leafhopper (*Erythroneura ziczac* Walsh) in British Columbia, although this would not provide absolute control since *E. ziczac* populations residing at the vineyard periphery (and beyond) could survive the tillage and then recolonize vines in the spring. De Valpine et al. (2010) evaluated a large, multi-year dataset of *E. elegantula* and Willamette mite (*Eotetranychus willametti* McGregor) populations in wine grape vineyards and found strong between-year synchrony in localized leafhopper populations, indicating that pest pressure at vineyard sites remained fairly consistent from year to year. It was concluded that this trend may be related to overwintering

processes or spatial variation in predator abundance. Such variation could likely be related to changes in landscape diversity and associated impacts on overwintering survival of *E. elegantula*.

During the growing season *E. elegantula* effectively escapes ground predators by residing in the crop canopy, yet in the winter it is forced to move into the more diverse vegetation on the vineyard floor in which it likely encounters a broader range of antagonists. Vineyards situated in more diverse landscapes may have increased populations of ground predators throughout the late fall, winter and early spring in the same way that increased landscape diversity is thought to lead to greater diversity and abundance of natural enemies in the vineyard during the summer.

Previous evaluations of *Anagrus* spp. overwintering habitat requirements have demonstrated that not all natural habitats necessarily provide suitable overwintering sites (Williams and Martinson 2000, Wright and James 2007, Lowery et al. 2007). Rather, *Anagrus* wasps appear to be limited to a small number of suitable overwintering host-plants, primarily plants in the Lamiaceae and Rosaceae. Given this information, it is less surprising that in this study the area of natural habitat did not specifically correlate with early-season *Anagrus* populations in vineyards. The assumption was that an increased area of natural habitat would likely correlate with parasitoid populations due to the increased probability of including suitable *Anagrus* spp. overwintering habitat in the overall area of "natural habitat". Obviously this was not the case. In this sense, "natural habitat" may be considered an overly broad predictor and a more refined metric of landscape diversity should be quantified that only includes "*Anagrus* overwintering habitat". At present such a well-defined quantification of *Anagrus* overwintering habitat is practically unattainable given the limited resolution of the vegetation cover type maps currently available.

Yet even with more refined data on landscape composition, the relationship between landscape diversity and early-season *Anagrus* populations in vineyards may not be linear to begin with. Insect capacity for movement and dispersal is determined by a variety of phenotypic and genetic factors, including organism size, trophic position, and resource specialization (Schellhorn et al. 2014, Tscharntke and Brandl 2004, Woiwood et al. 2001). While for larger insects body size can be a rough correlate of foraging range, the smallest insects that comprise the "aerial plankton" (such as aphids and thrips) are typically found to be widely dispersed throughout the landscape and thus somewhat unaffected by changes in landscape diversity (Gislen 1948, Tscharntke and Brandl 2004, Tscharntke et al. 2007).

Although little is known about the dispersal capacity and host-seeking behavior of *Anagrus* parasitoids, they likely do act as "aerial plankton" due to their extremely small body size. This was first hypothesized by Doutt and Nakata (1973), who observed earlier *Anagrus* colonization of vineyards that were down-wind from a large riparian habitat that was thought to be a key overwintering site for the parasitoids. Subsequently, Corbett and Rosenheim (1996a) used rubidium to mark *Anagrus* wasps that were overwintering on prune trees adjacent to vineyards and then re-captured wasps in the vineyard during the spring/summer. While they did find increased *Anagrus* populations on vines closer to the prune trees, only a small number (<30%)

contained the rubidium marker, indicating that a large proportion of the population was colonizing the vineyard from some other source. It was hypothesized that the increased *Anagrus* populations closer to the prune trees was actually due to the fact that these stands of trees were acting as a wind-break for wasps being transported across the landscape on wind currents (Corbett and Rosenheim 1996a). In a related study, Corbett and Rosenheim (1996b) marked *Anagrus* wasps by coating leaves that contained parasitized leafhopper eggs with fluorescent powder. The leaves were then placed in emergence containers in the center of a vineyard and the *Anagrus* wasps were marked upon eclosion from leafhopper eggs. The marked wasps were then recaptured on sticky-traps placed in a grid throughout the vineyard. Results indicated an *Anagrus* diffusion rate of 520 m^2/day, which is relatively rapid compared to other entomophagous arthropods (see Corbett and Rosenheim 1996b).

While limited in number, these preliminary assessments do provide some evidence of rapid aerial dispersal of *Anagrus* wasps and this could explain why proximity of overwintering habitat to vineyards may not entirely correlate with early-season parasitoids populations.

Results from this study indicated that *Anagrus* spp. was closely tied with *E. elegantula* populations regardless of landscape context. How do they find these leafhoppers? As an egg-parasitoid, *Anagrus* spp. must seek out a very inconspicuous host and, as such, has likely evolved a strong capacity to detect herbivore-induced plant volatiles triggered by leafhopper egg deposition and/or feeding (Fatouros et al. 2008, Hilker and Meiners 2006, Karban and Baldwin 1997).

Previous laboratory studies on *Anagrus* spp. have demonstrated that parasitoids in this genus do exhibit a strong response to chemical cues elicited by both herbivore oviposition (Chiappini et al. 2012) as well as feeding (Lou et al. 2005). While no similar work has been carried out to evaluate *Anagrus* spp. response to *Erythroneura* oviposition and feeding on grapes, field trials have been conducted in vineyards to evaluate their attraction to synthetic chemical lures that are formulated as analogs to some of the most common herbivore-induced plant volatiles (James 2005, James and Graswitz 2005, James and Price 2004, James 2003, Gadino et al. 2012). While in some cases *Anagrus* wasps were found in significantly greater abundance in the presence of these chemical lures (James and Grasswitz 2005, James 2005), at other times they were not (James and Price 2004, James 2003). One of the reasons for these inconsistent results likely has to do with the fact that little is known about the volatilization and dispersion of the chemical cues from these synthetic lures (Hunter 2002).

Given the evidence, it is very likely that *A. erythroneurae* and *A. daanei* both respond to herbivore-induced plant volatile chemicals as their primary method for host location in vineyards. As such, it may be that these wasps are effectively riding on wind currents and dropping into vineyards with *E. elegantula* populations throughout the growing season.

Results from this study indicate that *E. elegantula* populations are negatively correlated with increased landscape diversity and that, regardless of landscape diversity, it appears that *Anagrus*

spp. is successfully able to regularly locate and colonize vineyards with this pest. While this does have positive implications for biological control, parasitism by *Anagrus* spp. does not seem to effectively or consistently reduce late-season leafhopper populations. This is not to say that parasitism by *Anagrus* spp. is entirely irrelevant and, certainly, vineyards with low parasitism rates are very likely to see increased abundance of *E. elegantula* later in the season. Rather, findings from this study indicate that additional factors are driving *E. elegantula* population dynamics in North Coast vineyards, including seasonal population buildup and subsequent overwintering survival and these topics merit further investigation. Less diverse landscapes that are dominated by wine grape production are likely able to produce an abundance of overwintering leafhopper adults who are then subject to less overwintering predation due to a lack of habitat for natural enemies, in particular generalist predators. It appears that although *Anagrus* spp. can successfully colonize most vineyards, their ability to parasitize leafhopper eggs more rapidly than *E. elegantula* can produce them may be in question. Future studies are needed to more closely evaluate *Anagrus* spp. movement between overwintering sites and vineyards as well as their response to plant volatile cues from grape vines. Additionally, and more importantly, studies are needed to address the survival of overwintering *E. elegantula* in vineyards with varying levels of landscape diversity.

Chapter 5: Flowering cover crops attract natural enemies, but do not lead to enhanced biological control of pests in the vine canopy

ABSTRACT

California wine grape production is characterized by monoculture and specialized production. These systems can experience reductions in biological control due to the simultaneous concentration of habitat for crop pests and elimination of habitat for natural enemies. While previous studies have demonstrated that habitat diversification in agriculture can lead to increased natural enemy abundance and impact and/or reduced pest populations, well defined diversification practices are very specific to the crop and its pests and natural enemy complex. Many wine grape growers currently experiment with the use of cover crops to enhance biological control, although few reliable practices have been confirmed. This study evaluated the use of flowering summer cover crops to enhance biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn) in North Coast wine grape vineyards. Paired plots with and without flowering cover crops were compared over two years in multiple Napa and Sonoma County vineyards. Data were collected on natural enemy and pest densities, pest parasitism rates and crop yield and quality. Although increased natural enemy populations were observed on the flowering cover crops, this never translated into increased natural enemy density or impact on pests in the vine canopy itself. Alternately, it was shown that the proportion of natural habitat within 0.5 km of vineyard sites has a significant influence on natural enemy populations. Although flowering cover crops can attract natural enemies, they may require additional management in order to force movement of these organisms into the vine canopy.

INTRODUCTION

Modern agriculture is characterized by specialized crop production systems that are largely based in the use of monoculture cropping practices (Gleissman 2007). By maximizing the area devoted to a single crop species, resources for key phytophagous pests of these crops are highly concentrated in one particular area which allows them to more easily locate, colonize and proliferate in crop fields. At the same time, these simplified cropping systems lack many of the resources required to support natural enemies of crop pests, including refugia and overwintering sites, alternate hosts for parasitoids and alternate prey for predators, as well as nectar and pollen resources (Russell 1989, Landis et al. 2000). Working in combination, the simultaneous concentration of habitat for pests and elimination of habitat for their natural enemies can lead to reductions in the biological control of pests and increased pest outbreaks (Root 1973, Letourneau 1987).

The problems association with field scale crop simplification can be extended to a much larger spatial scale as well. As the development of monoculture cropping systems expands throughout an entire agricultural region, vast areas of land can become dominated by a small number of crop species and at the same time be devoid of natural habitats that can provide resources to support natural enemies of crop pests (Kruess and Tscharntke 1994, Duelli and Obrist 2003). Similar to what occurs at the field scale, the regional concentration of plant-host resources for phytophagous pests paired with the elimination of non-crop resources to support natural enemies can also lead to reductions in the biological control of crop pests (Tscharntke et al. 2005, Bianchi et al. 2006).

Like other modern agricultural systems, California wine grape vineyards are characterized by specialized production and the use of monoculture cropping practices. Geographic branding and the notion of "*terroir*" in many wine grape producing regions creates additional pressure to maximize vineyard acreage within a well-defined area and this is typically at the expense of natural and semi-natural habitats within these regions (Heaton and Merenlender 2000). California wine grape vineyards are thus very simplified both at the field scale (e.g., monoculture) as well as at the landscape scale (e.g., expansive vineyard development). As previously discussed, due to this lack of habitat diversity at both the field and landscape scale they are likely to experience degradation or even total loss of key ecosystem services such as biological control.

The Western grape leafhopper (*Erythroneura elegantula* Osborn [Hemiptera: Cicadellidae]) is a key pest of wine grapes in Northern California. *Erythroneura elegantula* adults overwinter in reproductive diapause in the leaf litter and on weedy vegetation in and around vineyards. When grape vines begin to develop new shoots in the spring (around early April), the adults move onto mature grape leaves where they feed and begin to oviposit into the leaves. In California'a North Coast wine grape region, these leafhoppers complete two generations per year before the adults enter back into diapause in the early fall and subsequently move back onto the vineyard floor as grape vines begin to senesce and lose their leaves.

The key parasitoids of *E. elegantula* are two species of Mymaridae wasp, *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *A. daanei* Triapitsyn. Both are solitary species that attack the eggs of *E. elegantula* and closely related species. Due to their lower degree-days requirements, these parasitoids can complete 2-3 generations for every one *E. elegantula* generation and can regularly build up large populations in vineyards during the growing season.

A number of generalist predators are also known to attack *E. elegantula*, including beetles in the family Cantharidae, *Chrysoperla* sp., *Geocoris* sp., *Hemerobius* sp., *Hippodamia convergens* Guérin-Méneville, *Nabis* sp., *Orius* sp., Syprhidae larva and spiders (Daane et al. 2013). Prior research has established that spiders are one of the most abundant generalist natural enemy in vineyards (>90% of the community in some cases) and thus one of the only natural enemy groups, other than *Anagrus* spp., thought to be present in sufficient densities to regulate *Erythroneura* leafhoppers (Costello and Daane 1999, 2003). Additional studies have indicated that *Orius* sp. may also play a role in the control of leafhoppers and thrips in North Coast vineyards (Nicholls et al. 2000, 2001).

In vineyards, a number of studies have evaluated the use of ground covers to increase biological control of *Erythroneura* leafhoppers. Wolpert et al. (1993) compared plots with orchardgrass (*Dactylis glomerata* L.) to clean cultivated grape vines. It was found that *E. elegantula* populations were significantly reduced in the presence of the orchardgrass and this was thought to be due to associated reductions in vine vigor, although natural enemy populations and parasitism rates were not measured in this study. Similarly, Daane and Costello (1998) compared vineyard plots with and without purple vetch (*Vicia benghalensis* L.) and barley (*Hordeum vulgare* L.) cover crops. While leafhopper populations were 15-20% lower in the cover crop plots, there was no associated increase in natural enemy populations or parasitism rates. Measures of vine vigor indicated that plots with ground covers showed significantly lower vigor as well as leafhopper egg deposition rates. As such, it was determined that leafhopper preference for vines with increased vigor, rather than natural enemy impact, had led to the differences observed between plots with and without cover crops (Daane and Costello 1998). Subsequent studies further confirmed leafhopper preference for more vigorous grape vines (Daane and Williams 2003)

Roltsch et al. (1998) evaluated the influence of weedy vegetation and cover crops on spider populations and biological control of the variegated leafhopper (*Erythroneura variabilis* Beamer) in a raisin grape vineyard. Cover crops included common vetch (*V. sativa* L.), purple vetch (*V. benghalensis* L.) and oat (*Avena sativa* L.). In this study presence of ground covers were associated with increased spider abundance and decreased leafhopper abundance in the vine canopy. In a related survey of spider population dynamics at multiple vineyard sites, it was noted that *E. variabilis* populations were the highest at a site where insecticide treatments had ostensibly eliminated spiders, potentially indicating the ecological release of leafhoppers from spider predation (Roltsch et al. 1998). Thus it was concluded that ground covers could increase spider populations in the vine canopy and their predation on leafhoppers could lead to decreased pest abundance.

Nicholls et al. (2000) evaluated the use of the flowering summer cover crops to enhance biological control of western grape leafhopper (*E. elegantula* Osborn) and western flower thrips (*Frankliniella occidentalis* Pergande). Flowering cover crop species included sunflower (*Helianthus annuus* L.) and annual buckwheat (*Fagopyrum esculentum* Moench). Cover crop plots were found to have lower populations of both leafhoppers and thrips as well as increased populations of generalist predators (esp. *Orius* sp., Coccinellidae beetles and Thomisidae spiders). There was no significant difference in leafhopper parasitism rates and *Anagrus* spp. populations were actually higher in control plots, which was thought to be the result of a density dependent response to the increased leafhopper population in these plots. Lower density of leafhoppers and thrips in the cover crop plots were thus attributed to impacts of generalist predators, namely spiders and *Orius* sp. Unlike previous cover cropping studies, Nicholls et al. (2000) also evaluated the impact of mid-season mowing of the flowering cover crops on pest and beneficial insect abundance in the vine canopy. They demonstrated that after mowing the flowering cover crops there was a significant increase in abundance (18%) of both generalist predators and *Anagrus* parasitoids in the vine canopy as well as a significant decrease (27%) in leafhopper nymph abundance (Nicholls et al. 2000, Altieri et al. 2005). Such results indicate that not just the presence of cover crops in vineyards, but rather their subsequent management throughout the growing season (i.e., timing of mowing) plays a critical role in their use as a habitat management strategy to enhance biological control of pests in the vine canopy.

Hanna et al. (2003) examined the impact of purple vetch (*V. benghalensis* L.), common vetch (*V. sativa*) and oat (*A. sativa* L.) on variegated leafhopper (*E. variabilis* Beamer). Paired plots with and without the cover crops also included vine exclusion sub-plots (to restrict spider movement between ground covers and grape vines) in order to better evaluate the impact of spider predation on leafhopper populations. As with previous studies, ground covers were not associated with any significant difference in leafhopper parasitism rates. While spider populations in the vine canopy were increased in the cover crop plots, this did not lead to any significant changes in leafhopper populations. Spider exclusion did result in a significant increase in leafhopper nymph populations, but only for the 1st generation. Hanna et al. (2003) concluded that although cover crops did enhance spider abundance, it was not sufficient enough to increase control of leafhoppers during the study period. In contrast to Daane and Costello (1998) and Costello and Daane (2003), the cover crop mix had no significant impact on vine vigor or nutrient status.

In a follow-up study, Costello and Daane (2003) re-evaluated the influence of cover crops on leafhopper populations. Using the same cover crops (purple vetch and barley) from their previous work (Daane and Costello 1998), this study attempted to isolate the relative influence of cover crops on vine vigor and natural enemy impact. Similar to Hanna et al. (2003), plots with and without the cover crops were compared with a third cover crop treatment plot that included spider exclusion from the vine canopy. Leafhopper populations were significantly reduced in both plots with cover crops, with the greatest reductions observed in the plots with cover crops and spider exclusion. There was no significant difference in parasitism rates between any of the plots nor any difference in spider populations in the non-exclusion plots with and without cover crops.

As in their previous study (Daane and Costello 1998), vine vigor was again shown to be significantly reduced in both plots with cover crops. These findings suggested that cover crops can influenced leafhopper populations by both reducing vine vigor and enhancement of natural enemies (Costello and Daane 2003).

Most recently, English-Loeb et al. (2003) assessed the use of buckwheat (*F. esculentum* Moench) and clover (*Trifolium repens* L.) to enhance biological control of *Erythroneura* leafhoppers. A laboratory trial was conducted to evaluate the influence of buckwheat nectar feeding on *Anagrus* spp. longevity and parasitism of sentinel leafhopper eggs. An associated field trial compared vineyard plots with buckwheat and clover with control plots containing only orchardgrass (*Dactylis glomerata* L.). Additional comparisons were also made between plots at the vineyard interior and edge (which was adjacent to a large woodland habitat). Results from the laboratory trial indicated that floral nectar feeding did significantly increase both the longevity of *Anagrus* wasps as well as leafhopper egg parasitism rates. Yet in the field trial parasitism of sentinel leafhopper eggs was significantly increased in the buckwheat plots in only one year of the study and overall leafhopper abundance did not appear to be consistently affected by the flowering cover crops. Furthermore, leafhopper distribution throughout the vineyard (edge versus interior vines) did not follow any consistent patterns.

Fewer studies have been conducted to evaluate the influence of landscape diversity on insect response in vineyards. Both Thomson and Hoffman (2010) and D'Alberto et al. (2012) evaluated the influence of landscape diversity on natural enemy populations in Australian vineyards. Landscape diversity was quantified at multiple spatial scales (95 – 3000 m radii around vineyard sites) and was defined by the proportion of woody habitat within each spatial scale. These studies found that spiders (D'Alberto et al. 2012) and other generalist predators (Thomson et al. 2010) did not exhibit any significant response to changes in landscape diversity, although Thompson and Hoffman (2010) did show that populations of Eulophidae wasps were found to positively correlate with increased landscape diversity while Trichogrammatidae and Mymaridae exhibited an opposite response. In California, Hogg and Daane (2013) evaluated how changes in landscape diversity influenced spider species composition in vineyards. Landscape diversity was quantified at multiple spatial scales (0.25 – 2 km) and defined by the proportion of agricultural and developed habitat within each spatial scale. Their findings indicated that an exotic invasive spider, *Cheircanthium mildei* Koch (Miturgidae), was much more dominant in vineyards situated in landscapes dominated by agricultural habitat and that increased landscape diversity could have implications for slowing the spread of invasive species.

Finally, only one study has ever compared how changes in on-farm habitat characteristics interact with changes in habitat diversity at the landscape scale. Isaia et al. (2006) evaluated the interaction between local and landscape variables by investigating the influence of landscape diversity on spider species composition in Italian vineyards under different management regimes that effected ground covers (no cover, minimal cover, and full cover). Spider species composition was calculated in terms of hunting strategy and landscape diversity was defined as the diversity of land-use types within a 200 m radius around each vineyard site. Sites were then categorized

as having either low, medium or high diversity landscapes. Changes in landscape diversity appeared to have the most significant influence on species composition, with an increase in ambush spiders and specialized predators and decrease in sheet web weavers in more diverse landscapes. There was no documented interaction between management regime and landscape diversity in this study.

As a whole, previous work on the use of cover crops to enhance biological control of *Erythroneura* leafhoppers has produced mixed results, although in some cases there is strong evidence that the addition of these ground covers can influence pest populations by enhancing natural enemy populations and/or decreasing crop vigor. Similarly, a much smaller body of literature has shown that in some cases natural enemy populations do respond to changes in landscape diversity, although mechanisms driving these outcomes remain unclear and no work has been conducted to evaluate how this impacts biological control of vineyard pests. More recently it has been proposed that on-farm, field-scale habitat diversification practices (like cover cropping) will likely be influenced by changes in landscape diversity (Tscharntke et al. 2005, Concepcion et al. 2008).

In North Coast vineyards, such an interaction between local and landscape habitat diversity likely effects biological control of *E. elegantula* by *Anagrus* wasps. The small size (< 1 mm) of *Anagrus* spp. make them very susceptible to desiccation and nutrient depletion, which is a serious risk in California vineyards where the Mediterranean climate results in long, dry summers and monoculture cropping practices significantly reduce the area and quality of suitable refugia (Landis et al. 2000, Segoli and Rosenheim 2013). Previous studies have shown that feeding on floral nectar (or analogous carbohydrates such as a honey-water solution) can significantly increase both the longevity and oviposition success of *Anagrus* wasps (English-Loeb et al. 2003, Segoli and Rosenheim 2013, Zhu et al. 2013). As such, habitat diversification at the vineyard scale may provide the necessary resources to allow *Anagrus* spp. populations to persist in vineyards. Additionally, while *E. elegantula* overwinter as adults in reproductive diapause, the *Anagrus* wasps overwinter as larva and are thus required to seek out an alternate leafhopper host that overwinters in an egg stage that they can effectively parasitize. For the most part these alternate hosts are located outside of vineyards in natural and semi-natural habitats (Doutt and Nakata 1965, Triapitsyn 1998, Lowery et al. 2007). In this way, vineyards located in landscapes that are dominated by agriculture and lack natural habitat may be less frequently colonized by *Anagrus* spp. with negative implications for biological control of *E. elegantula*. Given the importance of habitat diversity at both the field and landscape scale for *Anagrus* spp. populations, this study evaluates the ability of flowering summer cover crops to enhance biological control of *E. erythroneura* in vineyards situated in landscapes with low, intermediate and high levels of habitat diversity. By comparing plots with and without flowering cover crops in vineyards surrounded by varying levels of natural habitat, the performance of this field-scale diversification practice can be evaluated relative to changes in landscape diversity.

METHODS

Flowering cover crop treatment

Three species of flowering cover crop were selected for use in these trials, lacy phacelia (*Phacelia tanacetifolia* Benth. [Boraginaceae]), bullwort (*Ammi majus* [Apiaceae]), and wild carrot (*Daucus carota* [Apiaceae]). These species were chosen because of their known ability to attract a number of natural enemies, their sequential bloom sequence (Table 5.1), and their suitability for use in North Coast wine grape vineyards. All of the flowers are fall sown, drought tolerant and require no supplemental irrigation. The three species of flowering cover crops were sown together in alternate vineyard rows during the late fall (October/November) at a rate of 2.25 kg/species/hectare. Prior to sowing the seed, vineyard rows were tilled 1-2 times in order to prepare a seed bed for the flowers. A seed-drill with the outer two ports closed off was then used to sow the flowers at a depth of 3-5 cm in a tight strip (~40-60 cm wide) down the center of the vineyard row. After the sowing a ring-roller was used to ensure seed burial. With the onset of winter rains (~November/December), the flower seeds would begin to develop and seedlings could be seen as early as December at some of the research sites.

In the following year the *P. tanacetifolia* would begin to bloom in mid-April and reach peak bloom towards the end of that month. Following peak bloom, the stand of *P. tanacetifolia* would be mown at a height of 25-30 cm, which effectively killed it off and provided space for the next species of flower in the sequence to come up and bloom. The *A. majus* would begin to bloom in mid-May and reach peak bloom around 1 June. As with the *P. tanacetifolia*, the *A. majus* was mown at a height of 25-30 cm following peak bloom. The *D. carota* would then begin to bloom in early July and reach peak bloom in late July or early August. The *D. carota* was typically mown down to around 5 cm in early September in order to make space for workers and machinery harvesting the grapes.

Table 5.1 Flowering cover crop bloom period

Flower Species	Bloom Period
P. tanacetifolia	15 April – 5 May
A. majus	15 May – 30 June
D. carota	10 July – 1 September

Study sites

Field sites consisted of paired vineyard blocks >0.81 hectares (2 acres) located in Napa and Sonoma County, California, USA. All vineyard blocks were located on level ground and contained red wine grape varieties (Cabernet sauvignon, Merlot etc.) that were at least five years old. Each vineyard block typically consisted of 40-80 vine rows with 50-80 vines per row. Blocks were divided into two halves (20-40 rows each) and one of the halves was randomly designated as the "Treatment/Flowers" plot and the other as the "Control/Monoculture" plot. All samples were taken from the five vine rows in the middle of each experimental plot. Within each of the sample rows no measurements were taken from the first or last 10 vines. All plots were maintained insecticide free throughout the course of the study with the exception of mandatory insecticide

sprays in 2012 that were part of an eradication program for the invasive European grapevine berry moth (*Lobesia botrana* Denis & Schiffermüller [Tortricidae]) (Varela et al. 2010). These sprays consisted of non-contact products that are known to have low impacts on natural enemies and *Erythroneura* leafhoppers. Products used included insect growth regulators, diamides, microbial insecticides (e.g., *Bacillus thurigiensis*), avermectins and spinosyns.

Initially there were 11 study sites in 2012 and 9 sites in 2013, but due to poor establishment of the flowering cover crops data was only collected from eight sites in 2012 and two sites in 2013. A site with an effective treatment was defined as having had at least 2 of the 3 flowering cover crop species establish and bloom over at least 50% of the initial area sown to the flowers (i.e., 50% or more of the 40-60 cm strip in the row middle initially sown to the flowers). Flower establishment was assessed at peak bloom of each of the flowering cover crop species by randomly selecting 5 vines in the treatment plot and visually estimating the total percentage of flower establishment adjacent to the vine. This approach was also used to collect data on ground cover species composition in the control plots.

Natural enemies and leafhopper adults

Yellow sticky-traps were used to monitor *Anagrus* wasps, key generalist predators and *E. elegantula* adults between 15 April and 15 October each year. At each vineyard site, five yellow sticky-traps (16 x 10 cm; Seabright Laboratories, Emeryville, CA) were randomly assigned to vines within the sampling area and hung in the vine canopy. Traps were replaced approximately every two weeks.

Natural enemies on the cover crops

At peak bloom of each flowering cover crop species, sweep nets were used to sample the ground covers in the treatment and control plots at all sites (Table 5.2). Five samples were randomly collected from the ground covers in each plot at each site. Each sample consisted of 30 sweeps along a ~30 m transect starting at a randomly selected row and vine within the plot. Insects from each sample were stored in a plastic bag and brought to the laboratory. Samples were sorted under a dissecting microscope and all natural enemies were identified to family or genus.

Table 5.2 Dates of sweep net sampling the ground covers

Year	Flower bloom	Sample date
2012	*P. tanacetifolia*	22 April
	A. majus	14 June
	D. carota	2 August
2013	*P. tanacetifolia*	20 April
	A. majus	30 May
	D. carota	25 July

Leafhopper nymphs

Leafhopper nymph populations were monitored approximately once a week from 15 April to 15 October. On each sample date, 60 leaves were sampled from randomly selected vines at each

site. For the 1st generation of nymphs, leaves were sampled from shoot nodes 1-3. For the 2nd generation, leaves were sampled from shoot nodes 4-6, as the later generation of leafhoppers oviposit onto new vine growth. Each leaf was inspected on the top and bottom for leafhopper nymphs and total number of nymphs per leaf was recorded.

Egg parasitism rates

In a similar fashion, leafhopper egg parasitism rates were evaluated by collecting 30 leaves each from randomly selected vines at each site. Parasitism rates were assessed twice each season following peak nymph density of the 1st generation (~1-15 June) and 2nd generation (~20 July – 15 August). Leaves were collected from shoot nodes 1-3 for the 1st generation and nodes 4-6 for the 2nd generation. Leaves were brought to the laboratory and inspected with a dissecting microscope. Egg status was determined by the emergence mark present – a small slit in the egg close to the leaf surface indicated that a grape leafhopper had successfully emerged while 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 it was impossible to tell whether these eggs were healthy or parasitized.

Spiders in the vine canopy

In September of each year (Table 5.3), spiders were sampled from the vine canopy using a modified beat-sheet following Costello and Daane (1999). The beat-sheet consisted of a 1 m^2 cloth funnel that fed into a detachable plastic bag. Five samples were each collected from randomly selected vines at each vineyards site. Sampling involved holding the funnel beneath the grape vine canopy and vigorously shaking the vine for 30 seconds in order to dislodge spiders. All spiders were brought to the laboratory and identified to family.

Table 5.3 Dates of spider sampling in the vine canopy

Year	Sample Date
2012	12 September
2013	15 September

Vine vigor

Petiole total nitrogen (%) at peak bloom was quantified to assess vine vigor in 2012-2013. Peak bloom was defined as >80% of grape clusters in full bloom. At peak bloom, petioles were collected from 60 randomly selected vines at each site. Following Reisenauer (1978), each petiole was taken from opposite flower clusters near the base of a shoot. Only 1 petiole was collected from any given vine. Petioles were brought to the laboratory, washed with deionized water and dried at 55°C for 24 hours. Samples were then sent to University of California Division of Agriculture and Natural Resources Analytical Laboratory where total nitrogen levels were determined.

Crop yield and quality

Prior to crop harvest (< 24 hours), 10 vines per plot were randomly selected to assess yield and fruit quality. On each vine all grape clusters were counted and weighed to quantify total clusters

per vine and average cluster weight. To quantify crop quality, brix was measured from 3 composite samples of grape berries from the 10 randomly selected vines.

Quantification of landscape diversity

Landscape diversity was quantified by extracting "rangeland cover type" from the CalVEG dataset (US Forest Service 2010) using ArcGIS 10.1 (ESRI, Redlands, USA). There were 71 possible values for rangeland cover type (see Shiflet 1994 for descriptions). The total area of each cover type was calculated within a 500 m radius around each vineyard site. Cover types were then consolidated into 5 categories: "natural", "agriculture", "development", "water" and "no data". The proportion of cover by each category type was then calculated for each vineyard.

Summarizing the data

Data from the five yellow sticky-traps in each plot at each site were averaged for each sample period and then summed across "early-season" and "mid-season" sample dates (Table 5.4). The sum of these two data sets was then used to calculate "seasonal" abundance of pests and natural enemies on the sticky-traps.

Two separate analyses were conducted for "early-season" and "seasonal" data on natural enemies in order to determine whether or not the presence of flowering cover crops and/or changes in landscape diversity had any influence on natural enemy abundance over these two time periods. The "early-season" and "mid-season" sample periods for the yellow sticky-traps coincided with 1st and 2nd generation peak *E. elegantula* adult abundance respectively. Peak 1st and 2nd generation *E. elegantula* nymph abundance was determined by examining weekly nymph counts and identifying populations peaks. First and second generation *E. elegantula* adult and nymph abundance were strongly correlated and thus analyses on adults and nymphs were essentially redundant. For this reason only *E. elegantula* adult abundance was analyzed here (although data on nymph abundance is presented).

The five sweep net samples taken of each ground cover at peak bloom (Table 5.2) were summed for each plot at each site in each year (T = one measure per flower species bloom per plot per site per year for the sweep-net samples). Similarly, data from the beat samples of the vine canopy (Table 4) were summed for each plot at each site in each year of the study (T = one measure per plot per site per year for the canopy shake samples).

Natural enemy diversity was quantified using the Shannon-Weaver index (H'): $H' = - \sum (P_i * \ln P_i)$ where P_i is the fraction of the entire population made up of species *i*. A high value of H' would represent a more diverse and equally distributed community. A value of zero would represent a community with only one species.

Table 5.4 Yellow sticky-trap sampling periods

Period	Year	Sample Dates	Total Number of Approx. 2 Week Sample Periods	Cumulative Number of Days
Early-Season	2012	24 April – 6 June	3	43
	2013	12 April – 22 May	3	41
Mid-Season	2012	10 July – 21 August	3	42
	2013	14 July – 28 August	3	45

Statistics

Natural enemy and pest abundance from the yellow sticky-traps, parasitism rates, spider abundance from the beat sampling of the vine canopy, predator abundance from the sweep net samples of the ground covers, and all measures of crop vigor, yield and quality were evaluated with generalized linear models (GLMs). Most of the data in this study did not follow a normal distribution and was thus evaluated with GLMs that allow the specification of alternate error structures. As such, a negative binomial distribution was used for all count data and a quasibinomial distribution was used for proportional data in order to adjust for both the non-normal distribution as well as overdispersion of the data (Zuur et al. 2007, Crawley 2012). For each response variable, a full model was constructed that contained all possible explanatory variables and then likelihood ratio tests were used to evaluate the influence of individual explanatory variables via single term deletions ("drop1" command with X^2 tests [for negative binomial data] and F tests [for quasibinomial data] in package "lme4"). When data were normally distributed, a Gaussian (normal) error structure was used and single term deletion tests were evaluated with F tests. This is essentially the same as analysis of covariance. This type of analysis was used on all measures of total predator abundance, richness and diversity from the yellow sticky-trap data, spider abundance, richness, and diversity from the beat sampling of the vine canopy, as well as all measures of crop vigor and yield. All of the Gaussian and quasibinomial models were constructed using the "lme4" package and negative binomial models were constructed with the "MASS" package.

Data from both years of the study were pooled for analysis. All analyses of natural enemy abundance and parasitism rates included "proportion natural habitat within 0.5 km radius" and "Plot" as explanatory variables. Analyses of 1st generation *E. elegantula* adult abundance included "proportion natural habitat within 0.5 km radius", "Plot", "total petiole nitrogen (%)", and "early-season predator abundance" as explanatory variables. Analyses of 2nd generation *E. elegantula* adult abundance included the same variables as anlaysis of 1st generation adults, with the exception of "seasonal predator abundance" (rather than "early-season") and the addition of the explanatory variables "spider abundance" from the beat sampling of the vine canopy and "First generation parasitism rate". All data were analyzed with the statistics program R (version 3.0.3*, http://www.r-project.org/*).

Linear regression was used to evaluate how changes in landscape diversity influenced pest and natural enemy response to the flowering cover crops. The difference between plots with and

without flowering cover crops for each variable of interest was calculated as $Y_{Diff} = X_{Control} - X_{Flowers}$ where $X_{Control}$ is the value in the control plot without flowers and $X_{Flowers}$ is the value in the plot with flowering cover crops. Histograms were then used to evaluate the normality of Y_{Diff} (it was always normally distributed). Subsequently, linear regression was used to evaluate the relationship between Y_{Diff} and the "proportion of natural habitat within 0.5 km" of each site.

RESULTS

Establishment and composition of ground covers

With the exception of the *P. tanacetifolia* at one site in 2012 and the *A. majus* at one site in 2013, all three species of flowering cover crops effectively established and bloomed at all of the research sites used in this analysis (i.e., eight sites from the 2012 trials and two sites from the 2013 trials).

Weedy vegetation in the control plots typically consisted of a mixture of annual broad leaves and grasses, including common chickweed (*Stellaria media* [L.] Vill.), pigweeds (*Amaranthus* spp.) cheeseweed (*Malva parviflora* L.), mustards (*Brassica* spp.), medics (*Medicago* spp.), filarees (*Erodium* spp.), field bindweed (*Convolvulus arvensis* L.), tarweeds (*Hemizonia* spp.), prickly lettuce (*Lactuca serriola* L.), dandelion (*Taraxacum officinale* F.H. Wigg) and, to a lesser extent, sheperds purse (*Capsella bursa-pastoris* [L.] Medik.), lambsquarters (*Chenopodium album* L.), turkey mullein (*Croton setigerus* Hook.) and common purslane (*Portulaca oleracea* L.). Weedy vegetation was typically mown to ~5-10 cm in height in early May and again in July. Alternate rows in both treatment and control plots were tilled.

Summary statistics

Over the course of this two year study, yellow sticky-trap sampling produced a total of 5,405 *E. elegantula* adults (2,675 Control plot, 2,730 Flower plot), 6,457 *Anagrus* spp. (3,390 Control plot, 3,067 Flower plot) and 998 generalist predators (415 Control plot, 583 Flower plot). Sticky-traps also collected 998 generalist predators, of which there were 476 *Orius* sp. (159 Control plot, 317 Flower plot), 309 spiders (144 Control plot, 165 Flower plot), 111 *Syrphidae* (50 Control plot, 61 Flower plot), 73 Cantharidae (44 Control plot, 29 Flower plot), 15 *H. convergens* (11 Control plot, 4 Flower plot), 9 Chrysoperla sp. (4 Control plot, 5 Flower plot), 4 *Hemerobius* sp. (2 Control plot, 2 Flower plot), 1 *Geocoris* sp. (1 Control plot, 0 Flower plot), and 0 *Nabis* sp.

Sweep net sampling of the ground covers at peak bloom of the 3 flowering cover crop species yielded a large number of generalist predators. From the *P. tanacetifolia* 531 generalist predators (117 Control plot, 414 Flower plot), from the *A. majus* 1,200 generalist predators (161 Control plot, 1,039 Flower plot), and from the *D. carota* 347 generalist predators (41 Control plot, 306 Flower plot). Out of the 531 generalist predators on the *P. tanacetifolia*, there were 204 *Orius* sp. (17 Control plot, 187 Flower plot), 212 spiders (63 Control plot, 149 Flower plot), 48 *Chrysoperla* sp. (8 Control plot, 40 Flower plot), 25 Cantharidae (12 Control plot, 13 Flower plot), 19 *H. convergens* (11 Control plot, 8 Flower plot), 12 Syrphidae (4 Control plot, 8 Flower plot), 5 *Nabis*

sp. (2 Control plot, 3 Flower plot), 3 *Geocoris* sp. (0 Control plot, 3 Flower plot), and 3 *Hemerobius* (0 Control plot, 3 Flower plot). From the 1,200 generalist predators collected on the *A. majus*, there were 922 *Orius* sp. (110 Control plot, 812 Flower plot), 210 spiders (43 Control plot, 167 Flower plot), 33 *Nabis* sp. (3 Control plot, 30 Flower plot), 16 Chrysoperla (3 Control plot, 13 Flower plot), 7 *H. convergens* (0 Control plot, 7 Flower plot), 6 Syrphidae (2 Control plot, 4 Flower plot), 6 *Geocoris* sp. (0 Control plot, 6 Flower plot), 0 Cantharidae and 0 *Hemerobius* sp. Finally, out of the 347 generalist predators collected on the *D. carota* there were 215 spiders (25 Control plot, 190 Flower plot), 73 *Orius* sp. (7 Control plot, 66 Flower plot), 42 *Geocoris* sp. (9 Control plot, 33 Flower plot), 10 Syrphidae (0 Control plot, 10 Flower plot), 5 *Nabis* sp. (0 Control plot, 5 Flower plot), 2 Chrysoperla (0 Control plot, 2 Flower plot), 0 Cantharidae, 0 *Hemerobius* sp., and 0 *H. convergens*

Beat sampling of the vine canopy resulted in the collection of 182 spiders (71 Control plot, 111 Flower plot). Of those 182 spiders, there were 42 Miturgidae (15 Control plot, 27 Flower plot), 32 Corinnidae (11 Control plot, 21 Flower plot), 25 Salticidae (9 Control plot, 16 Flower plot), 21 Oxyopidae (6 Control plot, 15 Flower plot), 21 Theriidae (12 Control plot, 9 Flower plot), 16 Anyphaenidae (8 Control plot, 8 Flower plot), 9 Dictynidae (3 Control plot, 6 Flower plot), 7 Thomisidae (4 Control plot, 3 Flower plot), 0 Linyphiidae, 0 Gnaphosidae, 0 Desidae, 0 Lycosidae, 0 Agelinidae, and 9 unknowns (3 Control plot, 6 Flower plot).

Differences between flower and control plots: Natural enemy abundance on the ground covers

Relative to the weedy vegetation in control plots, the *P. tanacetifolia* attracted a significantly higher predator abundance (LRT = 16.4, p = <0.001) and diversity (F = 4.8, p = 0.04), but not richness (F = 1.1, p = 0.28) or evenness (F = 0.38, p = 0.55). In particular, *P. tanacetifolia* attracted significantly more Chrysoperla (LRT = 15.3, p = <0.001), *Hemerobius* sp. (LRT = 4.2, p = 0.04), *Orius* sp. (LRT = 12.3, p = <0.001), and spiders (LRT = 8.9, p = 0.003) relative to weedy vegetation in the control plots (Figures 5.1a and 5.2).

The *A. majus* also attracted significantly greater predator abundance (LRT = 11.6, p = <0.001) and richness (F = 11.7, p = 0.004), but not diversity (F = 2.3 p = 0.15). Predator evenness was actually significantly lower on the *A. majus* (F = 9.1, p = 0.009) compared to weedy vegetation. The increased predator abundance on the *A. majus* was characterized by significantly more *Geocoris* sp. (LRT = 6.4, p = 0.01), *H. convergens* (LRT = 8.3, p = 0.004), *Orius* sp. (LRT = 8.8, p = 0.003), and spiders (LRT = 12.7, p = <0.001) (Figures 5.1b and 5.2).

Predator abundance on the *D. carota* was significantly increased as well (LRT = 34.6, p = <0.001), along with species richness (F = 8.8, p = 0.009) and diversity (F = 13.7, p = 0.002), but there was no significant difference in predator evenness between *D. carota* and weedy vegetation in the control plots (F = 2.6, p = 0.13). *D. carota* was found to harbor significantly greater populations of *Orius* sp. (LRT = 28, p = <0.001) and spiders (LRT = 28.7, p = <0.001) (Figures 5.1c and 5.2).

Figure 5.1 Predator abundance on the ground covers. *P. tancetifolia* (5.1a); *A. majus* (5.1b); *D. carota* (5.1c).

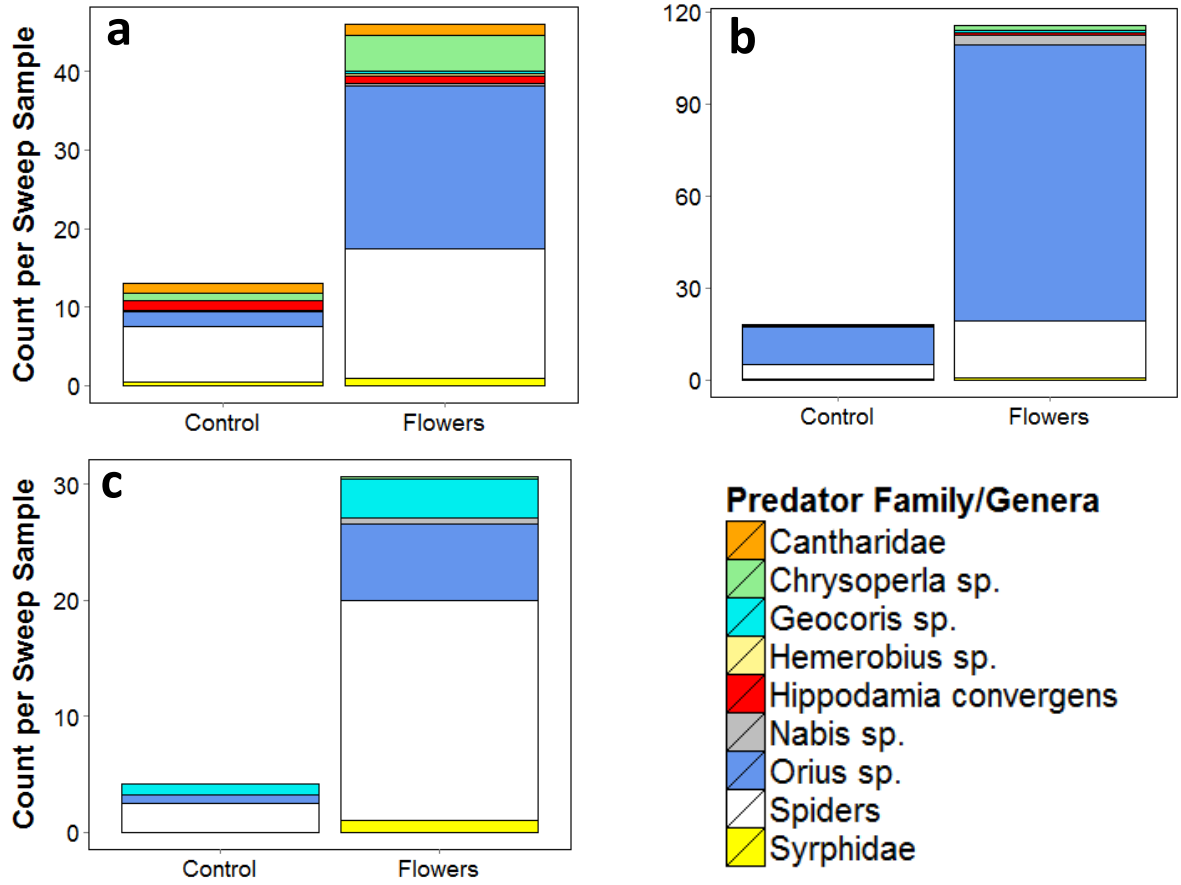
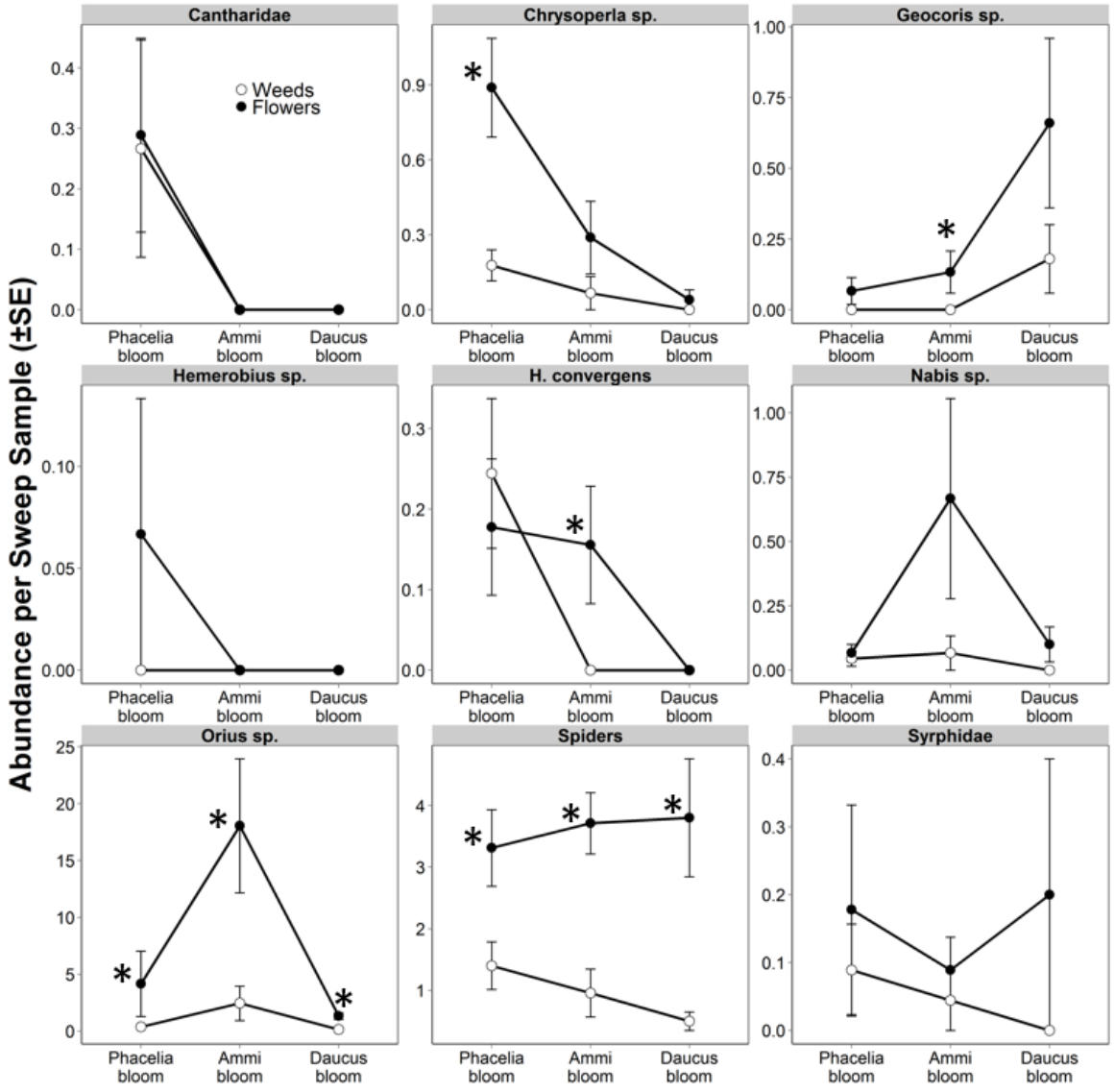


Figure 5.2 Predator family/genera abundance on the ground covers



Differences between flower and control plots: Natural enemies in the vine canopy – seasonal

Data from yellow sticky-traps in the crop canopy showed that overall predator abundance, species richness, diversity and evenness were all unaffected by flowering cover crops (Abundance $F_1 = 3.5$, p =0.08; Richness $F_1 = 3.4$, p = 0.08; Diversity $F_1 = 0.52$, p = 0.48; Evenness $F_1 = 2.9$, p = 0.11; Figure 5.3c). For the most part, individual predator families/genera were also unaffected by the flowers. One exception was *Orius sp.*, whose seasonal abundance was significantly higher in plots with flowering cover crops (LRT = 5.5, p = 0.02; Figure 5.4b). Similarly, seasonal *Anagrus* spp. abundance was not significantly influenced by flowering cover crops (LRT = 0.17, p = 0.68; Figure 5.4a). Analysis of the canopy shake samples indicated no significant influence of flowering

cover crops on spider abundance, richness, diversity and evenness were also not influenced by flowering cover crops (F = 3.1, p = 0.10; Figure 5.5).

Figure 5.3 Predator abundance in the vine canopy. Early season (5.1a); Mid-season (5.1b); Seasonal (5.1c).

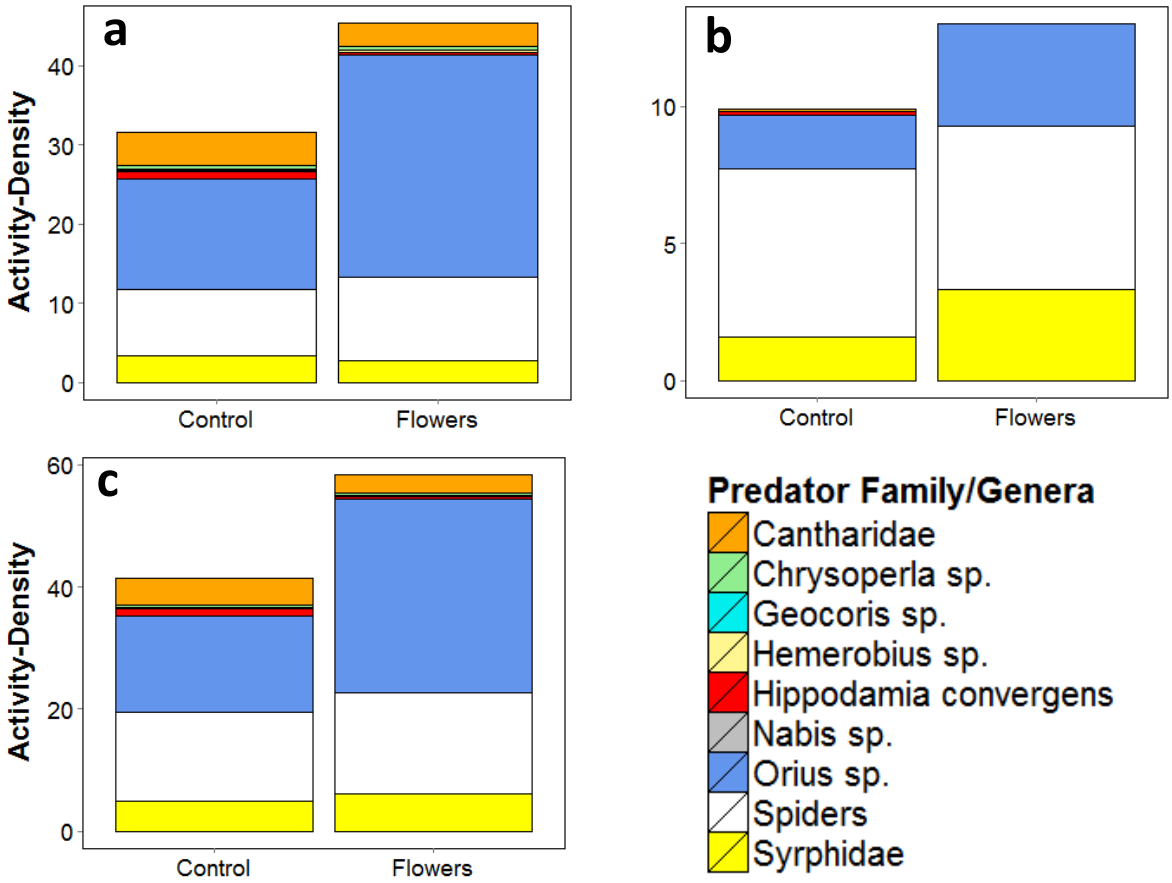


Figure 5.4 Seasonal natural enemy abundance in the crop canopy. *Anagrus* spp. (5.4a); *Orius* sp. (5.4b).

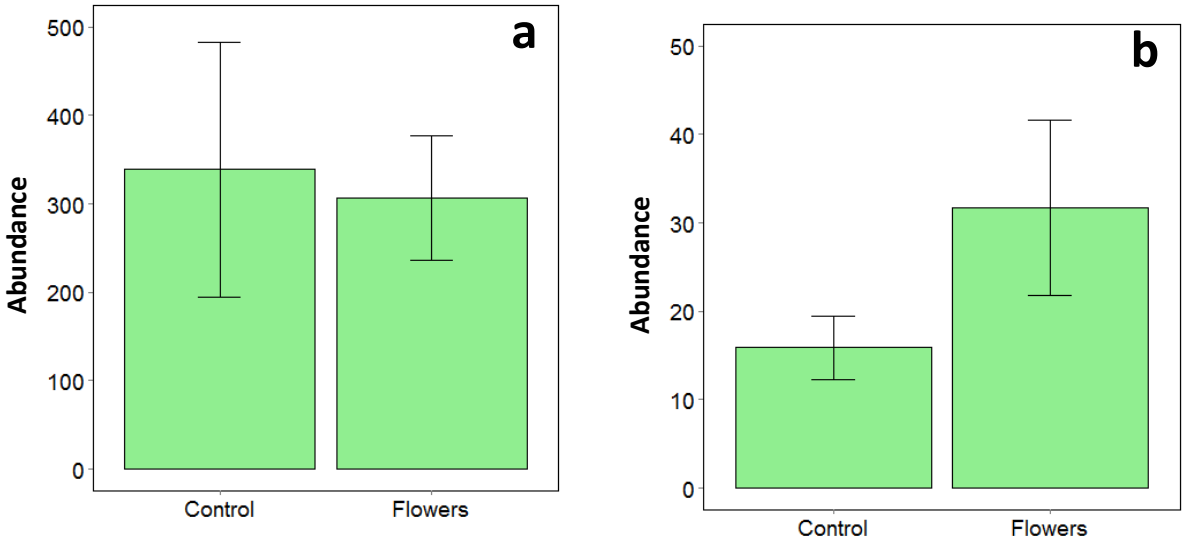
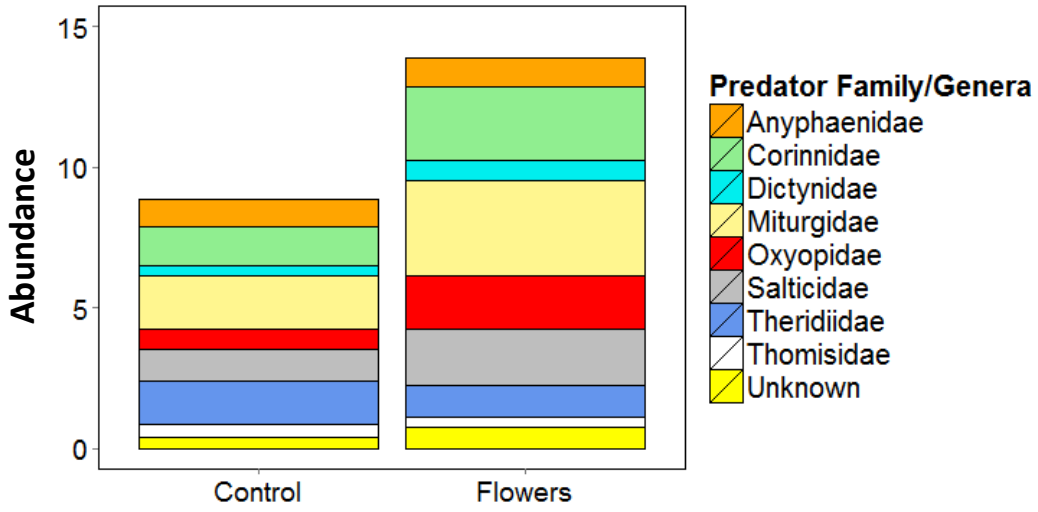


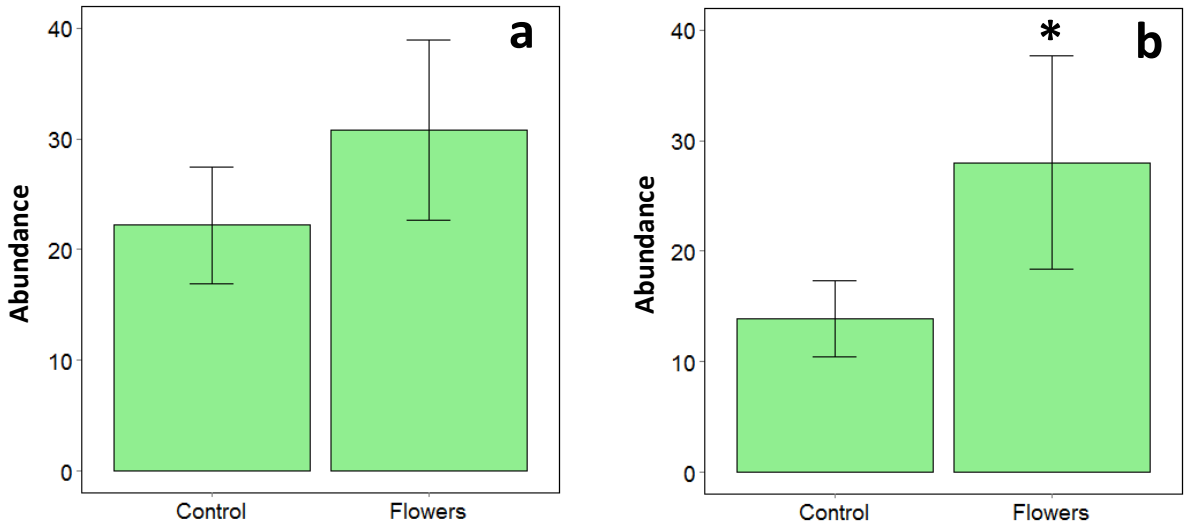
Figure 5.5 Spiders in the vine canopy.



Differences between flower and control plots: Natural enemies in the vine canopy – early season

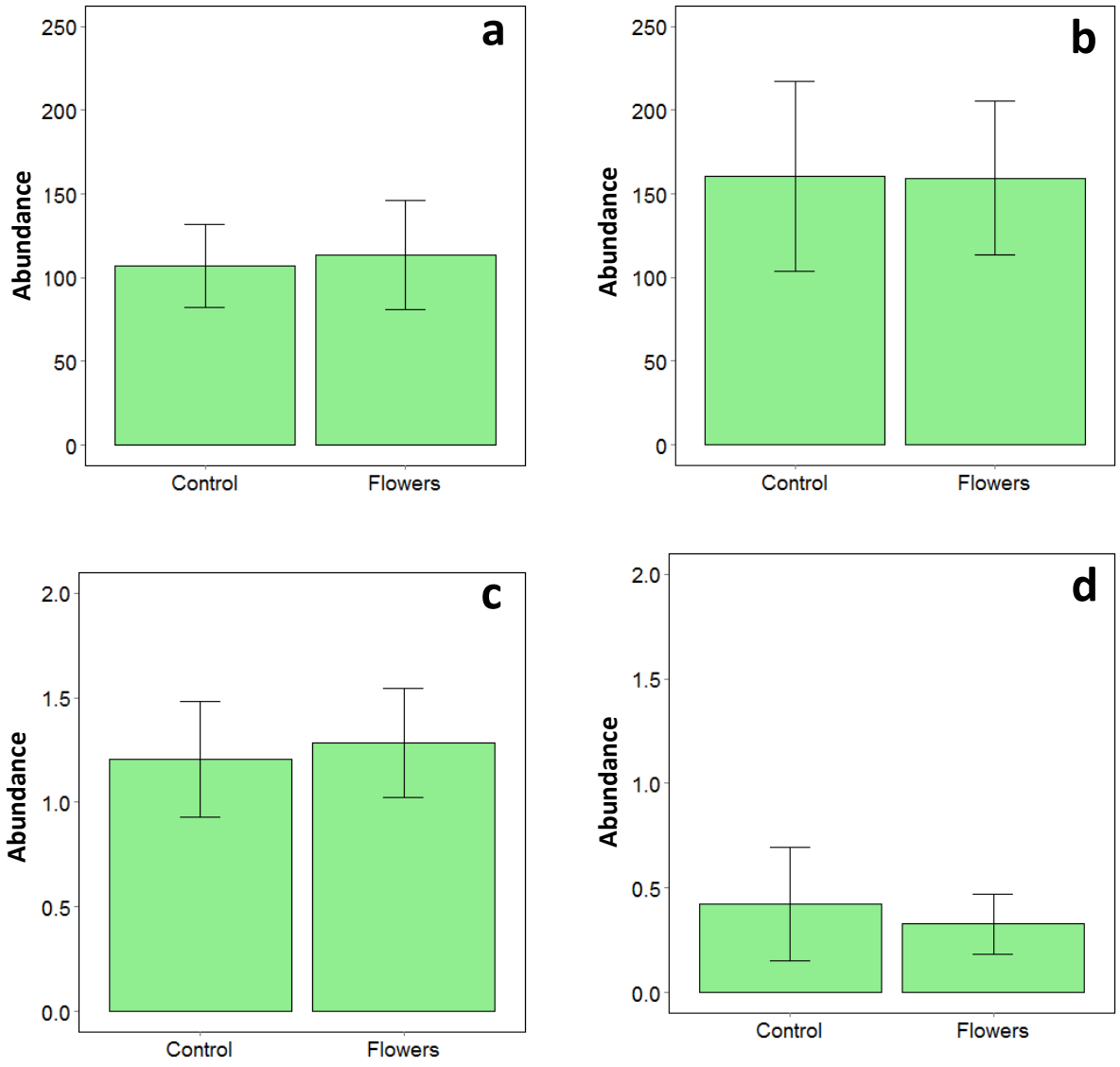
While early-season *Orius sp.* populations were significantly higher in plots with flowering cover crops (LRT = 4.5, p = 0.03; Figure 5.6b), overall predator abundance, richness, diversity and evenness were all unaffected by flowering cover crops (Abundance F = 2.6, p = 0.13; Richness F = 3.6, p = 0.07; Diversity F = 0.32, p = 0.58; Evenness F = 0.14, p = 0.71; Figure 5.3a). Early-season *Anagrus* spp. abundance was not influenced by flowering cover crops either (LRT = 0.49, p = 0.48; Figure 5.6a).

Figure 5.6 Early-season natural enemy abundance in the vine canopy. *Anagrus* spp. (5.6a); *Orius* sp. (5.6b).



Differences between flower and control plots: *Erythroneura elegantula* abundance
Flowering cover crops did not significantly influenced peak 1st or 2nd generation *E. elegantula* adult abundance (1st generation LRT = 0.03, p = 0.86; 2nd generation LRT = 0.05, p = 0.83; Figures 5.7a and 5.7b).

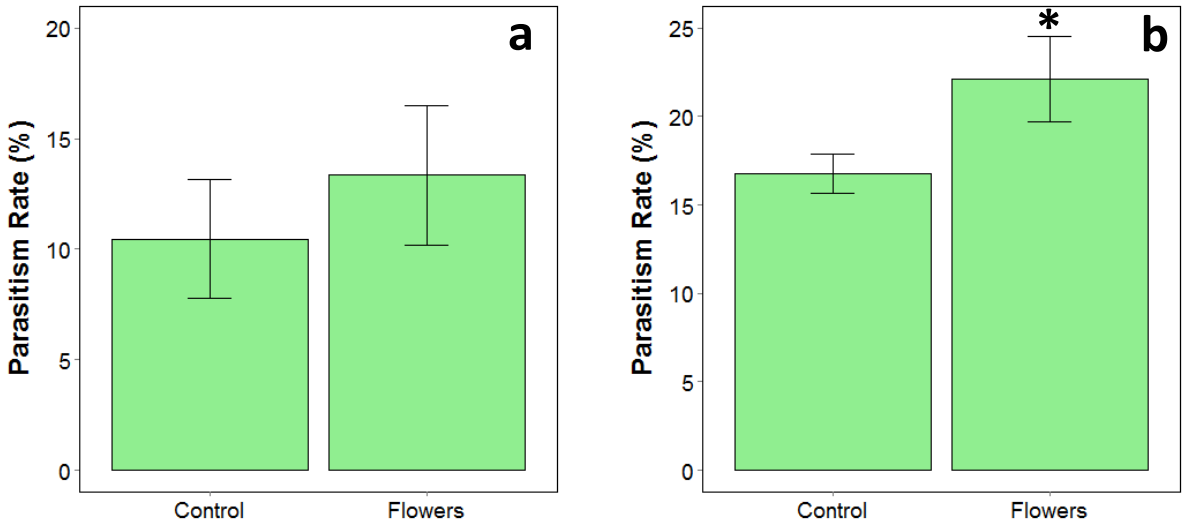
Figure 5.7 Peak *Erythroneura elegantula* abundance. First generation adults (5.7a); Second generation adults (5.7b); First generation nymphs (5.7c); Second generation nymphs (5.7d).



Differences between flower and control plots: Parasitism rate of leafhopper eggs

Parasitism of 1st generation leafhopper eggs by *Anagrus* spp. was not significant influenced by flowering cover crops (F = 0.72, p = 0.41; Figure 5.8a) but 2nd generation parasitism rates were significantly higher in the flowering cover crop plots (F = 11.3, p = 0.005; Figure 5.8b)

Figure 5.8. Parasitism of *Erythroneura elegantula* eggs by *Anagrus* spp. First generation (5.8a); Second generation (5.8b).



Differences between flower and control plots: Crop vigor, yield, and quality

Flowering cover crops did not reduce petiole total nitrogen (F = 0, p = 0.98; Figure 5.9a) or cane pruning weights (F = 0.27, p = 0.61; Figure 5.9b). Total numbers of clusters per vine, average cluster weight per vine and fruit quality (brix) were also not influenced by the flowering cover crops (Total clusters F = 0.007, p = 0.94; Cluster weight F = 0.04, p = 0.85; Brix F = 0.48, p = 0.50; Figures 5.10a, 5.10b and 5.10c).

Figure 5.9 Crop vigor was unaffected by the presence of flowering cover crops. Petiole total nitrogen content (5.9a); Cane pruning weights (5.9b).

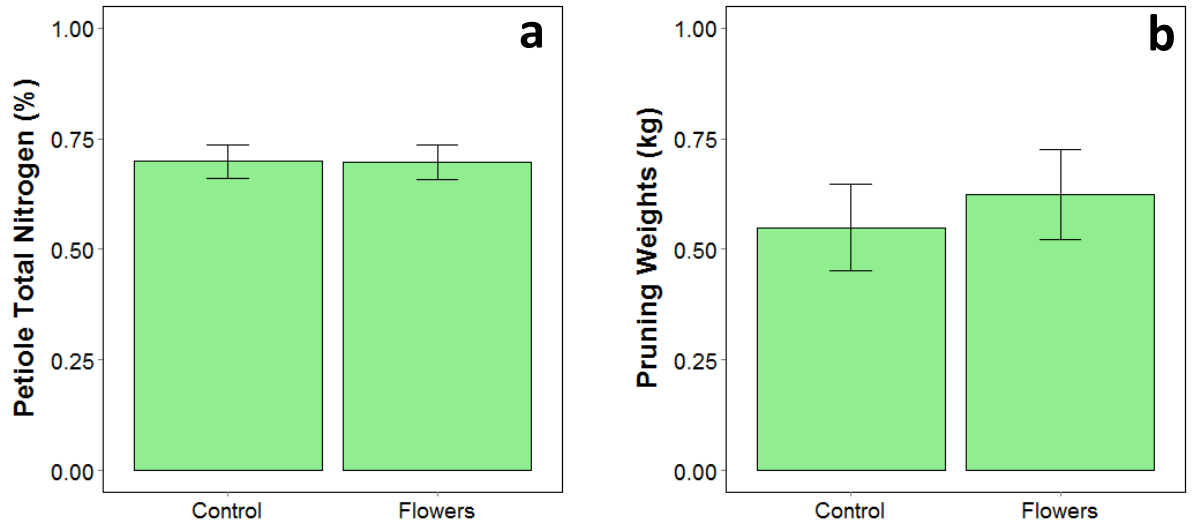
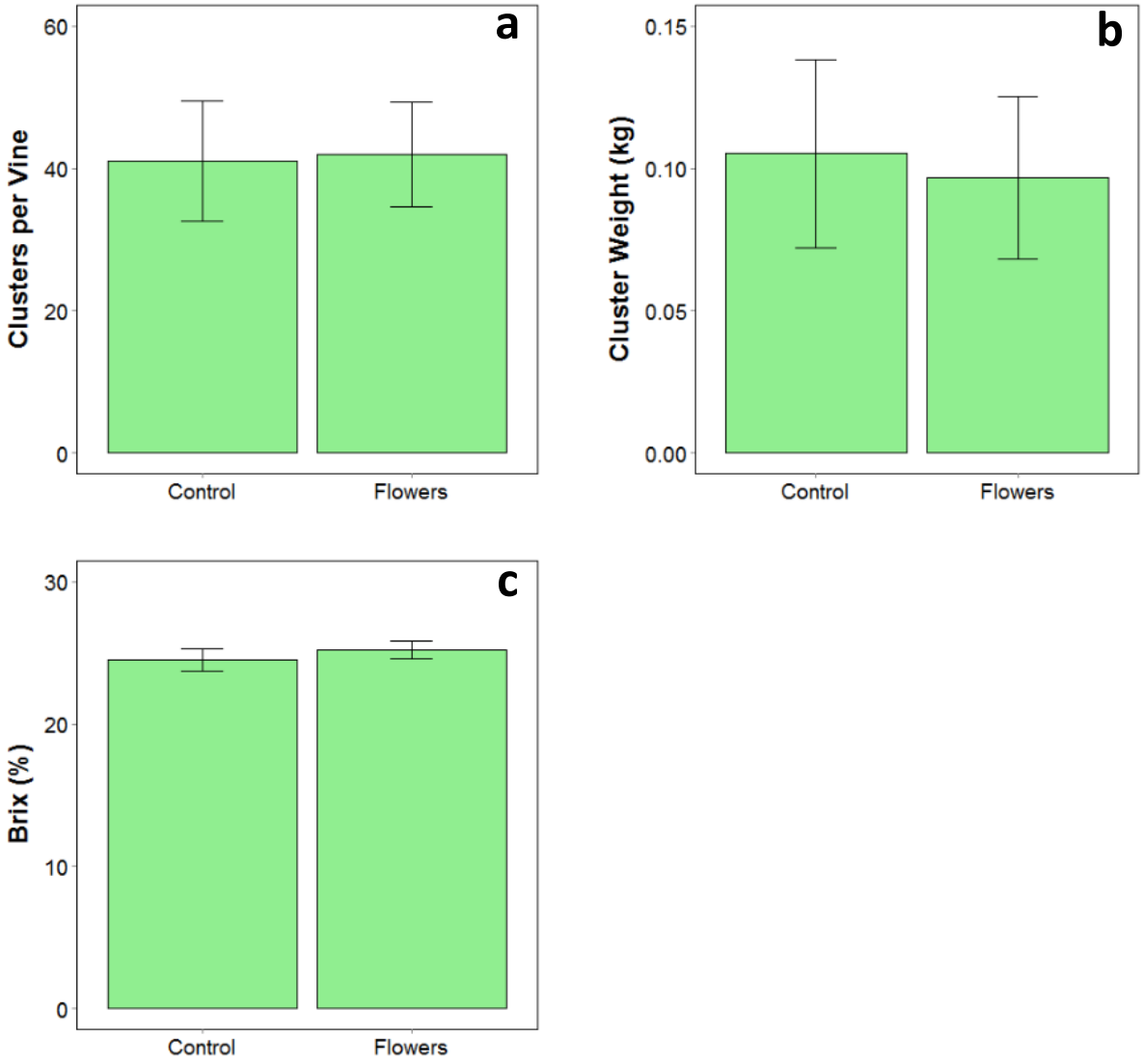


Figure 5.10. Crop yield and quality was unaffected by the presence of flowering cover crops. Clusters per vine (5.10a); Average cluster weight per vine (5.10b); Brix (5.10c).



Influence of landscape diversity on differences between flower and control plots: Natural enemy abundance on the ground covers

While all of the flowering cover crops harbored increased predator populations relative to weedy vegetation in the control plots, the difference in overall predator abundance between *A. majus* and weedy vegetation in the control plot grew even larger in more diverse landscapes (F = 30.1, p = <0.001; Figure 5.11b). There was no similar landscape effect on predator abundance for the *P. tanacetifolia* (F = 0.1, p = 0.76) or *D. carota* (F = 0.08, p = 0.79). Differences in species richness and diversity between each species of flower and paired weedy vegetation samples were also not influenced by changes in landscape diversity. Certain predators were found to be more abundant on the flowers in more diverse landscapes. Increased landscape diversity significantly increased populations of *Hemerobius* sp. on the *P. tanacetifolia* (F = 6, p = 0.04) as well as *Orius* sp. and spiders on the *A. majus* (*Orius* sp. F = 23.8, p = 0.002; Spiders F = 11.1, p = 0.01; Figure 5.12).

Figure 5.11 Influence of landscape diversity on predator abundance on the flowers and weeds. *P. tanacetifolia* (5.11a); *A. majus* (5.11b); *D. carota* (5.11c).

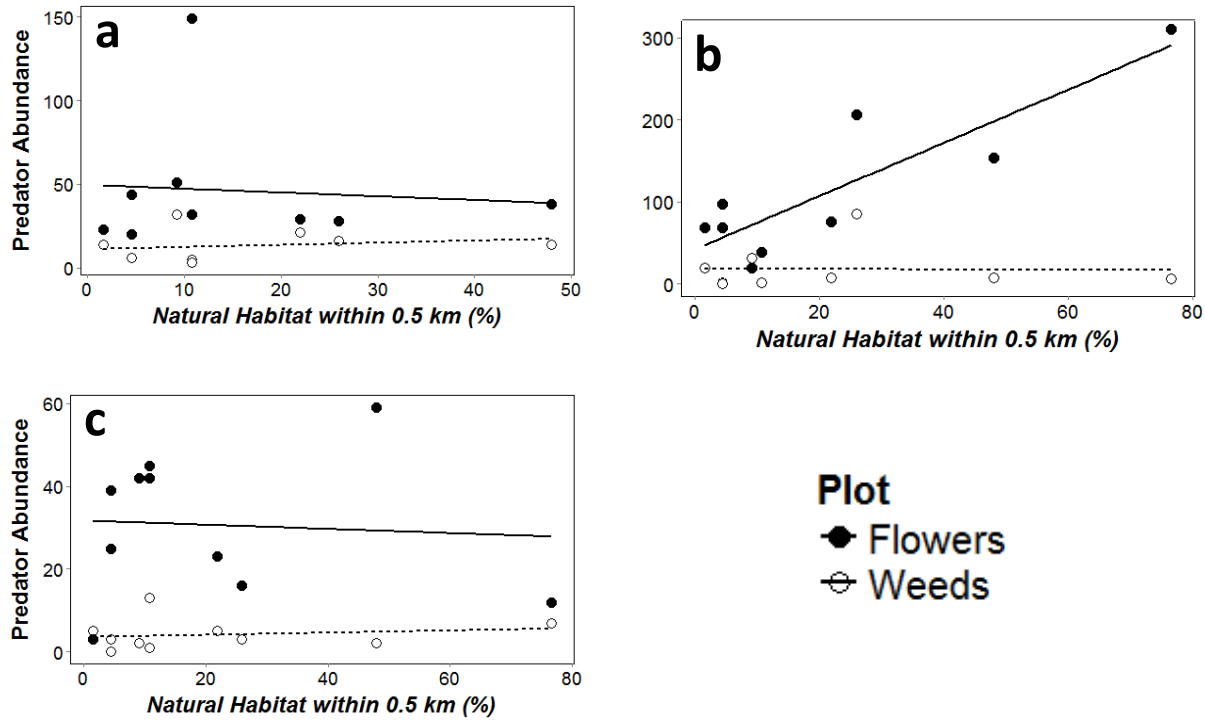
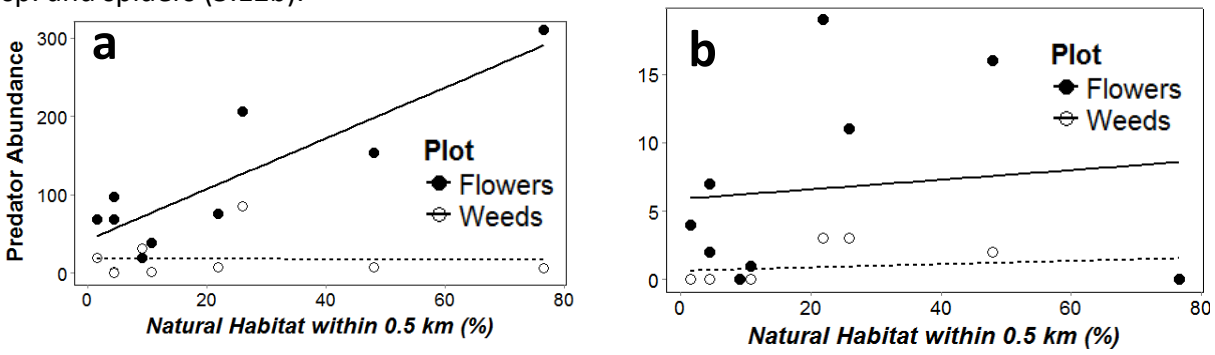


Figure 5.12 Increased predator abundance on *A. majus* in more diverse landscapes is primarily driven by *Orius* sp. and spider abundance. All predators (5.12a); All predators excluding *Orius* sp. and spiders (5.12b).



Influence of landscape diversity on differences between flower and control plots: Natural enemy abundance in the vine canopy

Differences in seasonal and early-season predator abundance, richness, and diversity in the crop canopy of flower and control plots were all not significantly influenced by changes in landscape diversity (Abundance-Seasonal F= 0.75, p = 0.41; Richness-Seasonal F = 0.06, p = 0.81; Diversity-Seasonal F = 3.7, p = 0.09; Abundance-Early F = 0.54, p = 0.49; Richness-Early F = 0.06, p = 0.81; Diversity-Early F = 2.8, p = 0.13). Similarly, seasonal and early-season differences between all of the individual predator groups were also unaffected by changes in landscape diversity. Differences in seasonal and early-season *Anagrus* spp. populations between the flower and control plots were also not significantly influenced by changes in landscape diversity (Seasonal F = 046, p = 0.51; Early F = 3.3, p = 0.11). Changes in landscape diversity did not produce any significant differences between the plots in terms of canopy spider abundance, richness or diversity either (Abundance F = 0.02, p = 0.89; Richness F = 0.17, p = 0.69; Diversity F = 0.20, p = 0.67).

Influence of landscape diversity on differences between flower and control plots: *Erythroneura elegantula* abundance

Landscape diversity had no significant effect on differences in 1st or 2nd generation *E. elegantula* adult activity or nymph populations between the flower and control plots (1st generation adults F = 0.08, p = 0.79; 2nd generation adults F = 0.40, p = 0.55; 1st generation nymphs F = 0.11, p = 0.75; 2nd generation nymphs F = 2.6, p – 0.14).

Influence of landscape diversity on differences between flower and control plots: Parasitism rates of leafhopper eggs

Differences in parasitism rates between flower and control plots were also unaffected by changes in landscape diversity (1st generation parasitism F = 0.47, p = 0.51; 2nd generation parasitism F = 0.02, p = 0.90)

Influence of landscape diversity on differences between sites: Natural enemy abundance in the vine canopy – seasonal

Overall predator abundance, species richness, diversity and evenness in the crop canopy at the vineyard sites were all unaffected by landscape diversity (Abundance $F_1 = 4.5$, $p = 0.05$; Richness $F_1 = 0.75$, $p = 0.40$; Diversity $F_1 = 0.03$, $p = 0.88$; Evenness $F_1 = 0.72$, $p = 0.42$). For the most part, individual predator families/genera were also unaffected by landscape diversity. One exception was *Orius sp.*, whose annual abundance was significantly higher at sites with increased landscape diversity (LRT = 6.4, p = 0.01; Figure 5.14). There was no significant influence of landscape diversity on spider abundance in the crop canopy (Abundance F = 4.1, p = 0.06), although spider species richness and diversity were both influenced by landscape diversity (Richness F = 7.8, p = 0.02; Diversity F = 6.9, p = 0.02; Figure 5.15). Seasonal *Anagrus* spp. populations were also not influenced by landscape diversity (LRT = 0.15, p = 0.70; Figure 5.13b), but were significantly influenced by *E. elegantula* abundance (LRT = 2.0, p = <0.001; Figure 5.13a)

Figure 5.13 Annual *Anagrus* spp. abundance showed a strong positive correlation with *Erythroneura elegantula* abundance (5.13a) but very little correlation with landscape diversity (5.13b).

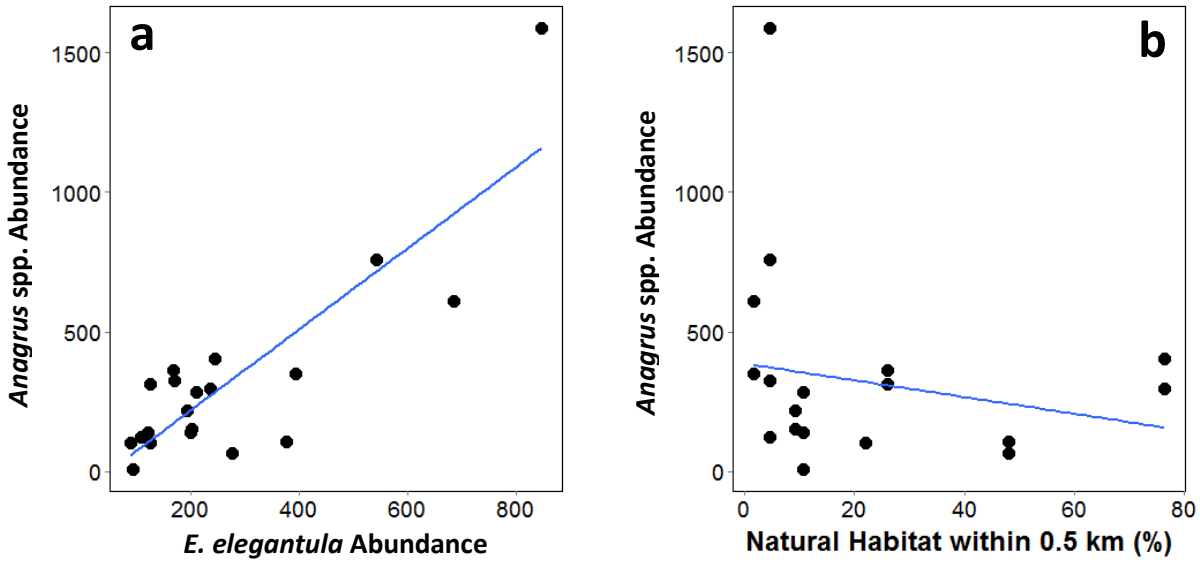


Figure 5.14 Seasonal *Orius* sp. abundance positively correlates with increased landscape diversity.

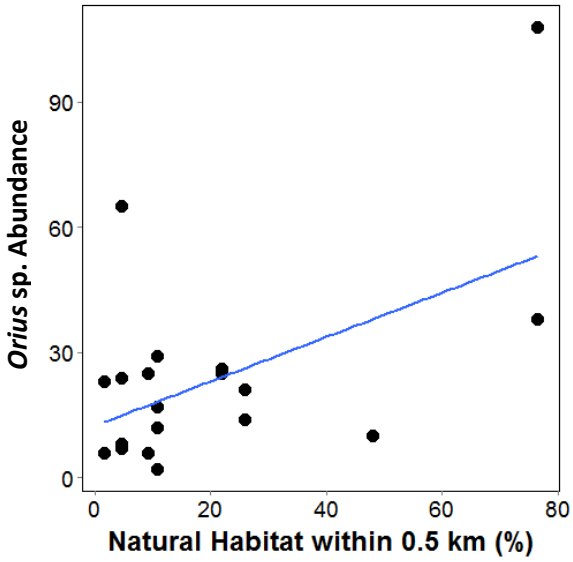
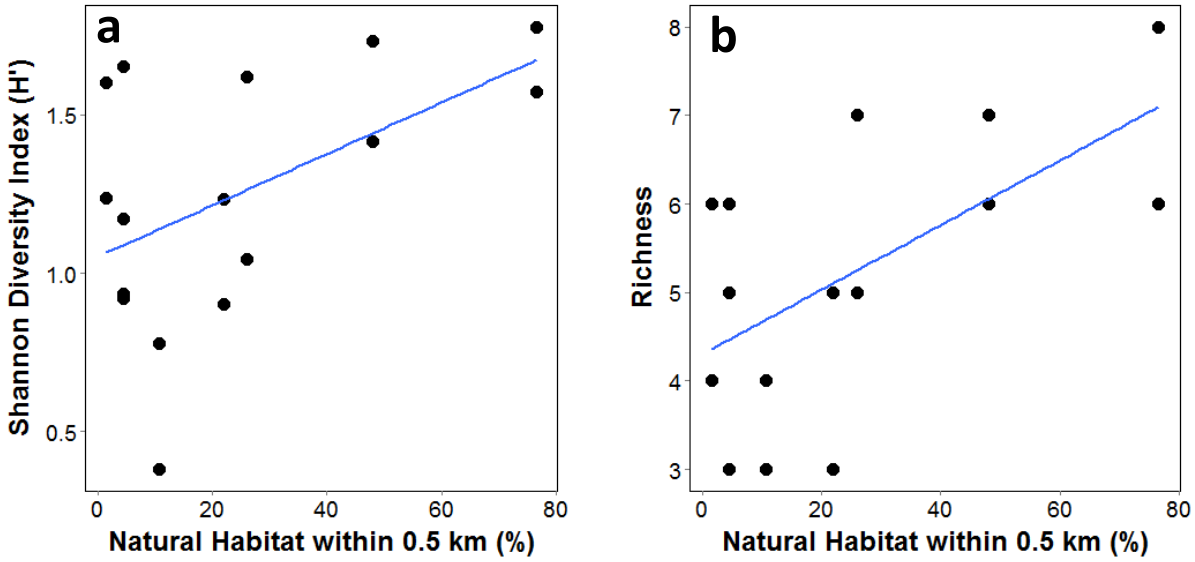


Figure 5.15 Diversity (5.15a) and richness (5.15b) of spiders in the vine canopy positively correlate with increased landscape diversity.



Influence of landscape diversity on differences between sites: Natural enemy abundance in the vine canopy – early-season

Early-season predator abundance was influenced by landscape diversity (F = 5.6, p = 0.03; Figure 5.16a), but species richness, diversity and evenness were all unaffected (Richness F = 0.28, p = 0.60; Diversity F = 0.07, p = 0.78; Evenness F = 3.8, p = 0.07). Early-season Cantharidae and *Orius sp.* populations were both significantly influenced by landscape diversity as well (Cantharidae LRT

= 6.7, p = 0.009; *Orius* sp. LRT = 4.5, p = 0.03; Figure 5.17). Early-season *Anagrus* spp. abundance was also influenced by landscape diversity (LRT = 15.7, p = <0.001; Figure 5.18a) as well as by *E. elegantula* abundance (LRT = 4.8, p = 0.03; Figure 5.18b).

Figure 5.16 Correlation between early-season predator abundance and landscape diversity is primarily driven by *Orius* sp. abundance. All predators (5.16a); All predators excluding *Orius* sp. (5.16b).

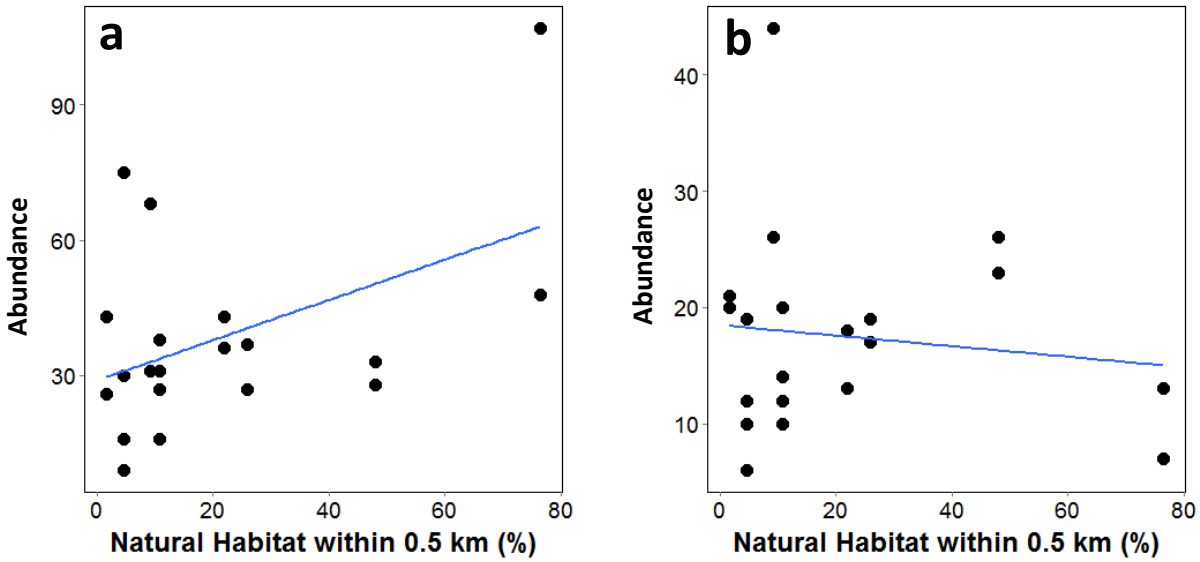


Figure 5.17 Early-season abundance of Cantharidae (5.17a) and *Orius* sp. (5.17b) correlated with changes in landscape diversity.

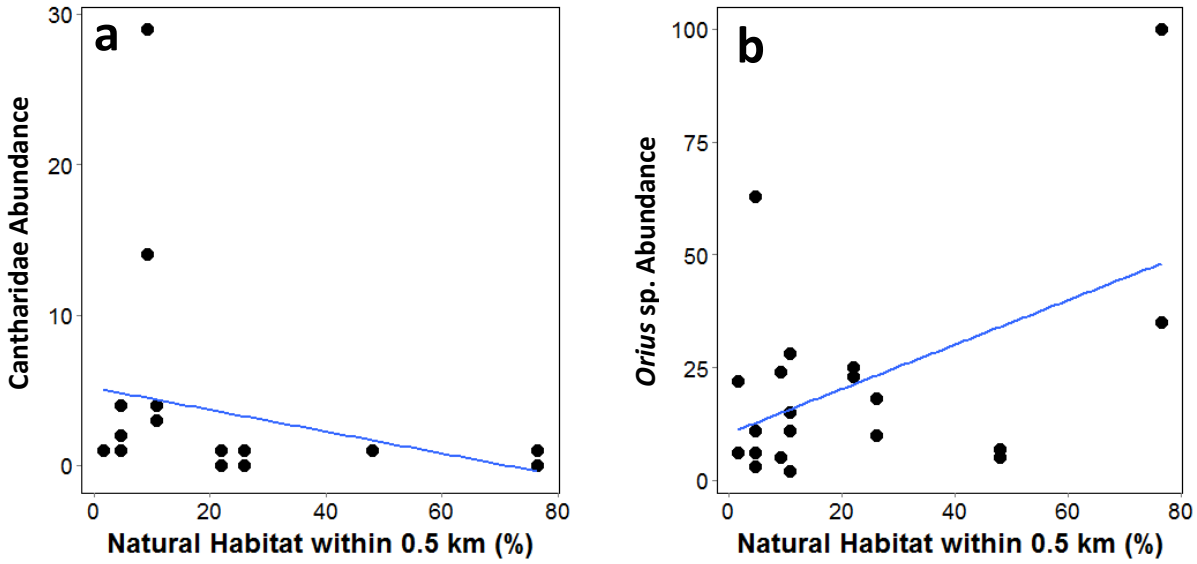
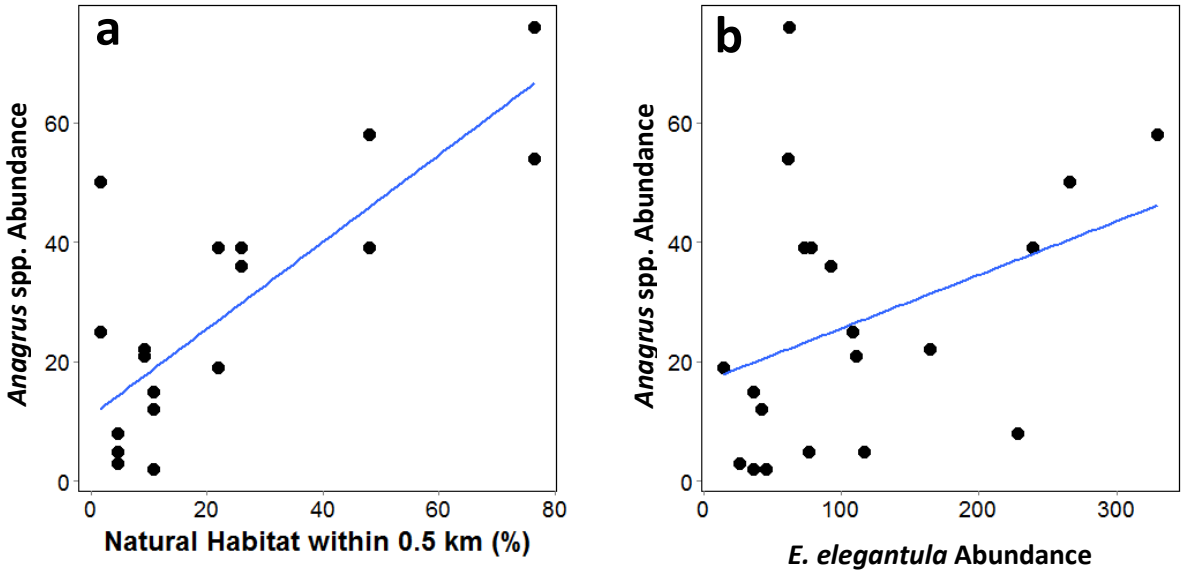


Figure 5.18 Early-season *Anagrus* spp. abundance correlated with both *Erythroneura elegantula* abundance (5.18a) as well as with changes in landscape diversity (5.18b).



Influence of landscape diversity on differences between sites: Parasitism rates of leafhopper eggs

Parasitism of 1st and 2nd generation *E. elegantula* eggs was not significantly influenced by landscape diversity (1st generation F = 3.9, p = 0.07; 2nd generation F = 3.1, p = 0.10).

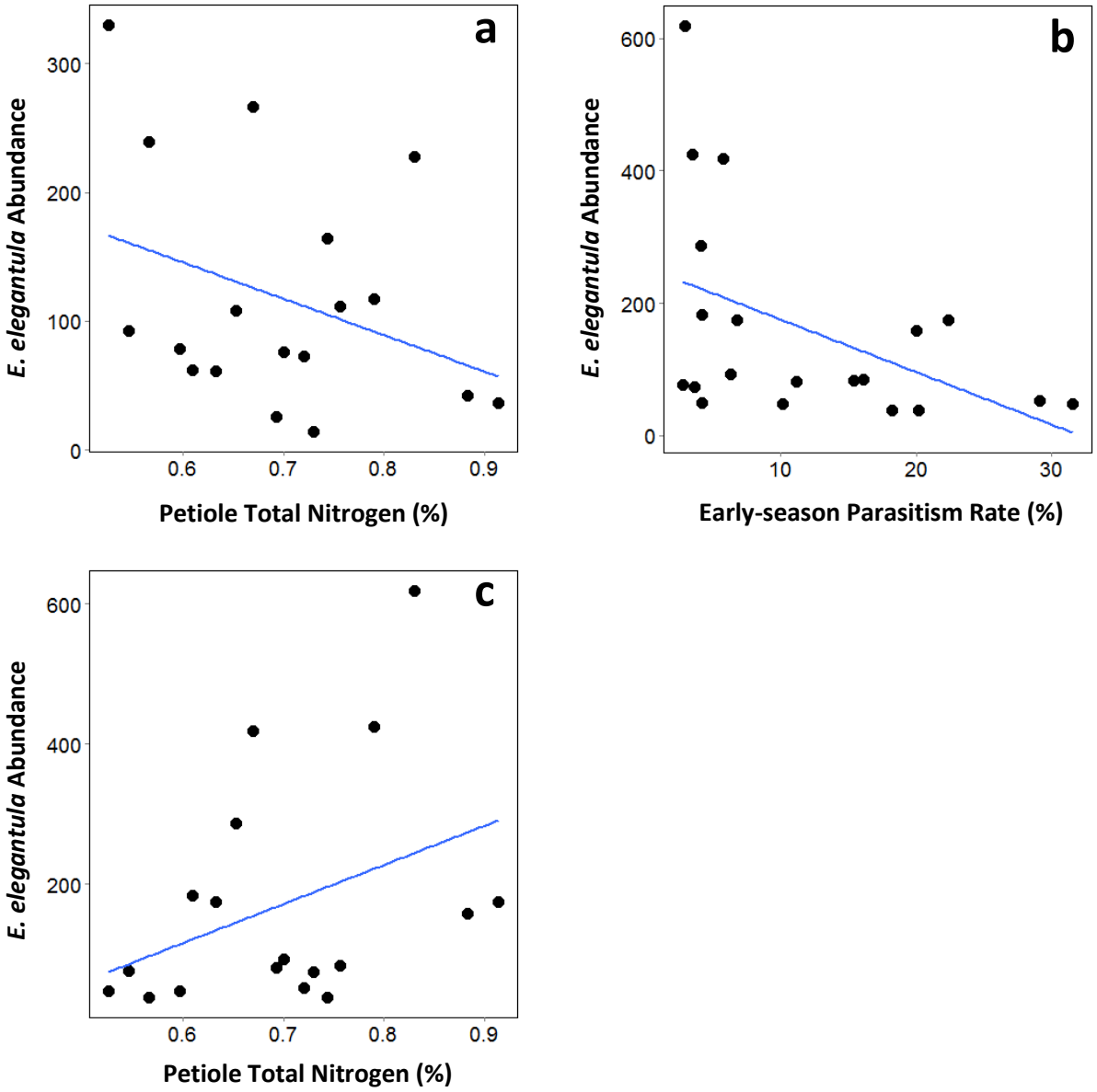
Influence of landscape diversity on differences between sites: *Erythroneura elegantula* abundance

Both 1st and 2nd generation *E. elegantula* adult abundance were not significantly influenced by landscape diversity (1st generation LRT = 1.6, p = 0.20; 2nd generation LRT = 1.6, p = 0.20).

Influence of crop vigor, natural enemy abundance and parasitism rates on *Erythroenurae elegantula* abundance

1st generation *E. elegantula* adult abundance was significantly influenced by petiole total nitrogen content (LRT = 4.1, p = 0.04; Figure 5.19a). 2nd generation *E. elegantula* adult abundance was significantly influenced by high early-season parasitism rates (LRT = 4.6, p = 0.03; Figure 5.19b) as well as total petiole nitrogen content (LRT = 5.5, p = 0.02; Figure 5.19c).

Figure 5.19 Abundance of first generation *Erythroneura elegantula* adults is influenced by petiole total nitrogen content (5.19a) while abundance of second generation *Erythroneura elegantula* adults is influenced more by early-season parasitism rate (5.19b) than petiole total nitrogen content (5.19c).



DISCUSSION

In this study, flowering cover crops attracted a more diverse and abundant population of generalist predators relative to the weedy vegetation in paired control plots. These findings closely match with those of Nicholls et al. (2000) who in a similar vineyard trial observed increased predator abundance, especially *Orius* sp., on the flowering cover crops buckwheat (*Fagopyrum esculentum* Moench) and sunflower (*Helianthus annus* L.) compared with weedy vegetation in control plots. Yet in this study increased predator diversity and abundance on the flowering cover crops never appeared to translate into significantly higher predator activity in the vine canopy itself. Similarly, no significant difference in *Anagrus* spp. abundance was observed between plots with and without the flowering cover crops. Given these findings, it is not surprising then that there were subsequently no significant differences in *E. elegantula* abundance or 1st generation parasitism rates between the flower and control plots, although parasitism of 2nd generation leafhopper eggs was significantly higher in the flowering cover crop plots.

These findings are similar to previous vineyard cover cropping trials in which the presence of ground covers was found to have no significant or consistent effect on natural enemy populations in the vine canopy (Daane and Costello 1998, Costello and Daane 2003, English-Loeb et al. 2003), although Costello and Daane (2003) argued that differences in spider species composition, rather than overall abundance, could have implications for biological control. While Hanna et al. (2003) and Roltsch et al. (1998) both found increased spider abundance in plots with cover crops, it could not be demonstrated that this led to any significant change in leafhopper populations. The only vineyard cover crop study to see a change in both natural enemy and pest populations in the crop canopy was Nicholls et al. (2000), who found increased generalist predator populations (but not *Anagrus* spp.) in plots with flowering cover crops and concluded that such increases were likely responsible for the observed reduction of both thrips and grape leafhoppers (Nicholls et al. 2000). Furthermore, Nicholls et al. (2000) took the additional step of mowing the flowering cover crops in order to force movement of natural enemies from the cover crop into the vine canopy. Taking measurements of pest and natural enemy abundance in the vine canopy before and after the mowing, they found that mowing the cover crops did lead to an increase in natural enemy abundance and decrease in pest abundance in the vine canopy (Nicholls et al. 2000). Thus, it may be that additional management of cover crops is necessary in order for them to have an impact on biological control of pests. Rather than simply use flowering cover crops to attract natural enemies into a vineyard, the cover crops may require further management in order to "push" natural enemies up into the vine canopy.

A key goal of this study was to evaluate not only the ability of flowering cover crops to enhance biological control of *E. elegantula*, but to determine whether or not the effectiveness of this on-farm diversification practice was at all influenced by changes in landscape diversity. As such, it was demonstrated that some flowering cover crops do attract a greater abundance of certain natural enemies in more diverse landscapes (e.g., *Orius* sp. and spiders on *A. majus*; Figures 5.11 and 5.12). The stronger response of *Orius* sp. and spiders to the *A. majus* in more diverse

landscapes may be due to the fact that this flower blooms right around the beginning of the seasonal "dry down" that occurs in natural habitats in a Mediterranean climate. As the quality of these natural habitats diminishes due to the onset of seasonal drought, the floral resources in the vineyards become one of the few floral resources that is still available in the environment. Vineyards located in high diversity landscapes are thus surrounded by natural habitats with large populations of natural enemies in search of flowering plant resources. A response may have been detected for *Orius* sp. and spiders in particular because these are the two most abundant predators found in this system. A similar response may have occurred for other natural enemies, but was not detected due to low overall abundance. In the same way, vineyards in low diversity landscapes are likely experiencing a similar out-migration of natural enemies from natural habitats, but in much lower abundance due to the limited amount of habitat in these regions and thus a smaller response to the flowers was observed. Yet beyond these trends in natural enemy abundance observed on the flowering cover crops themselves, the influence of the flowers on pest and natural enemy populations in the vine canopy did not appear to vary with changes in landscape diversity. Thus whether or not the vineyard was located in a simple or diverse landscape, the flowering cover crops failed to significantly enhance natural enemies in the vine canopy and/or influence biological control of *E. elegantula*. Again, as seen in Nicholls et al (2000), it may be necessary to further manage cover crops in order to force movement of natural enemies up into the vine canopy (e.g., by mowing).

Both early-season as well as seasonal *Anagrus* spp. populations were positively correlated with, respectively, early-season and seasonal *E. elegantula* adult activity. Due to its rapid developmental time (2-3 generations for every *E. elegantula* generation), *Anagrus* spp. is known to exhibit a density-dependent response to *E. elegantula* populations and this was likely what was observed in this study. Alternately, it could be that *Anagrus* wasps actively colonize vineyards in response to herbivore-induced plant volatiles (HIPVs) that are produced by grape vines in response to feeding and/or oviposition by *E. elegantula* (Karban and Baldwin 1997). Previous studies in vineyards have evaluated the use of synthetic chemicals that are formulated as analogs to the herbivore-induced plant volatiles released by plants under herbivore attack (James 2003, James and Price 2004, James 2005, James and Graswitz 2005, Gadino et al. 2012). In some cases *Anagrus* wasps were found to positively respond to these chemical lures (James 2005, James and Grasswitz 2005), but not always (James 2003, James and Price 2004). As such, this latter explanation remains in question. Regardless of ground cover type, vineyards with increased area of natural habitat within 0.5 km were found to have higher early-season *Anagrus* spp. populations. This is likely due to the fact that these natural habitats contain suitable overwintering sites for the *Anagrus* spp. and vineyard proximity to them allows for earlier colonization by these parasitoids and in greater numbers. Similarly, *Orius* sp. abundance was also increased in vineyards with high levels of landscape diversity. The increased abundance of *Orius* sp. in more diverse landscapes is likely due to the increased availability of refugia, alternate prey and nectar/pollen in the natural habitats around these vineyards (Landis et al. 2000). Second generation *E. elegantula* abundance was significantly higher in vineyards with low 1st generation parasitism rates. While all vineyards did experience some degree of early-season parasitism (thus indicating the presence of *Anagrus* spp. in all vineyards), it may be that the vineyards with low

parasitism rates simply had an *Anagrus* spp. population that was too small and/or arrived too late to have any significant impact on biological control over the course of the season. As mentioned, increased area of natural habitats around a vineyard site likely allow for greater and more frequent colonization by *Anagrus* spp., not only early in the season but throughout the year. Although the dispersal ability of *Anagrus* spp. continues to remain an outstanding question (Antolin and Strong 1987, Corbett and Rosenheim 1996a, 1996b, Reeve and Cronin 2010), it is likely that due to their minute size they commonly disperse on air currents in a somewhat uncontrolled fashion, what is sometimes referred to as "aerial plankton" (Gislen 1948, Doutt and Nakata 1973, Russell 1999). In this way, vineyards situated in landscapes with little to no natural habitat (and thus lacking *Anagrus* spp. overwintering sites) may still be colonized by *Anagrus* spp. (and thus experience some early-season parasitism) although it will likely be much less frequent and in lower abundance (as was observed in this study). In light of the fact that these wasps do tend to exhibit a density-dependent response to *E. elegantula,* it may be that small populations of the wasp may not be able to effectively parasitize enough host eggs to significantly increase their population and, in turn, have little effect on biological control of *E. elegantula* over the course of the season. This would be even more likely to occur in the face of increased local extinction pressure due to intensive cropping practices with little possibility for vineyard re-colonization in less diverse landscapes. While populations of *Orius sp.* were also increased in more diverse landscapes, their impact on *E. elegantula* populations in this study is less clear since predation pressure was not quantified. Similar vineyard trials have indicated that *Orius* sp. can have a significant impact on *E. elegantula* nymphs (Nicholls et al. 2000, Altieri et al. 2005) and this may have further contributed to the reductions in 2nd generation *E. elegantula* populations observed here. That said, increased *Orius* sp. populations were also observed in plots with flowering cover crops where no significant change in *E. elegantula* populations was observed.

Second generation *E. elegantula* populations were also positively influenced by crop vigor. *Erythroneura elegantula* preference for vigorous grape vines has been previously demonstrated in a number of studies (Mayse et al. 1991, Wolpert et al. 1993, Daane et al. 1995, Daane and Williams 2003) and in some cases the influence of cover crops on pest populations has been shown to be a function of reduced crop vigor in the presence of cover crops (Daane and Costello 1998, Costello and Daane 2003). Other vineyard cover cropping studies have shown that petiole NO_3 was unaffected by the presence of cover crops (Hanna et al. 2003). In this study, flowering cover crops did not appear to influence vine vigor. Cover crops also had no significant influence on crop yield or fruit quality. The observed differences in crop vigor between the experimental sites may be related to differences in soil quality, moisture, soil fertility management and/or irrigation regime, factors which were not specifically controlled for in this study.

Surprisingly, 1st generation *E. elegantula* populations were negatively correlated with crop vigor. This may be due to the fact that 1st generation leafhopper populations are effectively an artifact of the population from the previous season and that as overwintering adults emerge in the spring they simply feed on the grape vines in their immediate vicinity. Population response to increased nitrogen in the crop may not really be noticeable until later generations. Insect preference for more nutritious and/or vigorous host plants is thought to be related to the fact that they are N-

limited (White 1974, McNeil and Southwood 1978, Mattson 1980, Price 1991). Feeding on hosts with elevated nitrogen levels can shorten developmental time and increase reproductive success (Mattson 1980, Awmack and Leather 2002, Altieri and Nicholls 2003) which would mean that the beneficial effect of feeding on more nutritious plant material would not necessarily be noticeable until subsequent generations (i.e. 2nd generation *E. elegantula* populations).

High early-season populations of *E. elegantula* are generally tolerated by growers in the North Coast due to the fact that biological control by *Anagrus* spp. is fairly consistent in this region. Early season *E. elegantula* activity in the vineyard typically attracts some population of *Anagrus* spp. that in most cases can rapidly increase in abundance and effectively keep leafhopper populations in check for the remainder of the year. Where early-season biological control is insufficient, *E. elegantula* populations will likely reach outbreak proportions by the mid-season (2nd generation) and it is at this point in the year when many growers will make a decision about whether or not to apply a chemical pesticide to control them. As such, 2nd generation *E. elegantula* adult abundance is arguably one of the most important measures of leafhopper pest pressure over the growing season.

In this study, the addition of flowering cover crops did successfully attract a more abundant and diverse population of natural enemies. Unfortunately, natural enemies on the flowers never appeared to actually move into the vine canopy and there was no observable difference in biological control of pests in plots with and without the flowering cover crops. Rather, early-season *Orius* sp. and *Anagrus* spp. activity in the vine canopy was positively correlated with increased landscape diversity, indicating a significant role of the landscape on vineyard natural enemy populations. Subsequently, high early-season parasitism rates of leafhopper eggs had a negative influence on 2nd generation *E. elegantula* populations and, at the same time, high levels of crop vigor appeared to have a positive influence on 2nd generation *E. elegantula* abundance. These findings indicate that high vigor vineyards situated in low diversity landscapes may be more likely to experience pest outbreaks due to a combination of (a) low levels of biological control by *Anagrus* wasps and (b) crop conditions that promote the development of *E. elegantula* populations. Use of flowering cover crops should not be ruled out entirely though, as their ability to attract a diverse and abundant population of natural enemies does have positive implications for biological control of pests. As previously mentioned, it may be necessary to further manage cover crops in order to force natural enemy movement into the vine canopy. Furthermore, the fact that flowering cover crops were shown to have no influence on crop vigor, yield or quality makes them a suitable option for growers interested in vineyard habitat diversification. Whether or not flowering cover crops can be managed in a way that allows for the enhancement of biological control, some growers may be interested in their use for conservation or aesthetic purposes alone.

While habitat diversification is important for the maintenance of ecosystem services to agriculture (Altieri 1999, Landis et al. 2000, Kremen and Miles 2012) it is critical to understand how biodiversity should be arranged in space and in time in order to most effectively and reliably enhance these services (Kremen 2005, Moonen and Barberi 2008). The ability of on-farm habitat

diversification practices to enhance biological control has, to date, produced mixed results (Andow 1991, Letourneau et al. 2012) and it is possible that in some cases the performance of these localized diversification treatments was significantly altered by having been evaluated in an inappropriate landscape context (Tscharntke et al. 2005). Alternately, it may be that in some cases habitat diversification is meaningful for biological control only at a landscape-scale. Vineyard cropping systems may be a good example of this, as the overwintering biology of *Anagrus* spp. creates a unique situation in which biological control of *E. elegantula* is almost entirely contingent on the presence of perennial non-crop habitat that can serve as adequate overwintering sites for *Anagrus* spp.

Chapter 6: Conclusion

Main Findings

Although many natural enemies were attracted to the flowering cover crops, it appears that their addition to the vineyard does not significantly enhance biological control in any way, regardless of landscape context. Alternately, results from these studies did indicate that the natural habitats found in the landscapes surrounding North Coast vineyards have a very significant influence on *Anagrus* spp. populations and biological control of the Western grape leafhopper (*Erythroneura elegantula* Osborn). Findings from each of the studies are summarized according to the key questions that were originally posed in the Introduction:

What are the specific host plants utilized by *Anagrus* spp. in the landscape?

The key *Anagrus* parasitoids of *E. elegantula* are attacking alternate leafhopper host eggs on a limited number of specific host plants in the natural habitats surrounding vineyards. More specifically, *Anagrus erythroneurae* S. Trjapitzin & Chiappini was predominantly reared from *Baccharis pilularis* DC. and *Rubus* spp. while *A. daanei* Triapitsyn was reared only from *Vitis californica* Benth. and *Rubus* spp. These findings indicate the importance of natural habitat quality in terms of plant species composition rather than gross area. Furthermore, in some cases it appears that leafhoppers on these plants serve as hosts for the *Anagrus* not just during the overwintering period, but throughout the entire year. These populations residing outside of the vineyard may potentially serve as source-pools of *Anagrus* wasps that can re-colonize vineyards following a localized extinction during the growing season.

To what extent do biological control services extend out from patches of natural habitat?

The influence of vineyard proximity to riparian habitat on pest densities appeared to be mediated by changes in crop vigor rather than biological control by natural enemies. Reduced crop vigor was observed in vineyard areas adjacent to patches of riparian habitat and these same areas tended to have lower *E. elegantula* egg deposition and nymph densities. Natural enemy populations and pest parasitism rates did not exhibit any distinct spatial trend relative to the riparian habitat and thus it was concluded that lower pest densities adjacent to the riparian habitat were the result not of natural enemy impact but rather due to *E. elegantula* preference for more vigorous grape vines at the interior of the vineyard.

What is the influence of landscape diversity on biological control in vineyards?

Erythroneura elegantula densities were decreased in landscapes with greater habitat diversity but this did not appear to be mediated by natural enemy impacts during the growing season. While early season densities of *Anagrus* spp. were found to vary between vineyard sites, there was no clear relationship with the landscape and they showed strong density dependence with *E. elegantula* populations. It appears that these tiny (<1 mm) parasitoids may be able to disperse over great distances in order to locate *E. elegantula* in vineyards. Lower early season populations of *E. elegantula* in more diverse landscapes is thought to be attributed to predation of overwintering adults, although follow-up studies are necessary to evaluate this.

Does landscape diversity mediate the ability of flowering cover crops to enhance biological control?

Although flowering cover crops attracted a lot of natural enemies, there was no difference in natural enemy densities in the crop canopy between treatment and control plots. The flowers could attract a lot of natural enemies, but this never translated into increased densities in the crop canopy, much less any enhancement of biological control. The influence of the flowers did not appear to correlate in any way with changes in landscape diversity. Essentially, the flowers performed poorly in all landscapes. There is some evidence from previous studies (Nicholls et al. 2000) that indicates mowing of the cover crops may be one way to force natural enemy populations up into the crop canopy, but that was not explored here.

Sites in more diverse landscapes were found to have significantly higher densities of *Anagrus* spp. in the early season, which subsequently led to increased *E. elegantula* parasitism rates which was then correlated with lower late season *E. elegantula* densities. As opposed to the findings from Chapter Three, here it appears that increased landscape diversity can lead to increased natural enemy populations and impacts.

Future Directions

Future studies should try to incorporate *Anagrus* spp. overwintering habitat into the quantification of landscape diversity. Rather than evaluate *Anagrus* response to the proportional area of natural habitat surrounding vineyard sites, a new metric that calculates the proportional area of overwintering habitat surrounding study sites would be much more appropriate and useful. Much remains unknown about the movement and dispersal of *Anagrus* wasps across the landscape. While current mark-recapture methods have already been used for the study of *Anagrus* dispersal at the field scale (Corbett and Rosenheim 1996a, 1996b), nothing has been attempted at the landscape scale. If these wasps are indeed dispersing as “aerial plankton”, then it would be appropriate to make an attempt at quantifying this movement. Obviously it is of interest to know about *Anagrus* movement from overwintering sites into the vineyards, but it would also be intriguing to evaluate how spillover of these wasps from the vineyards influences population dynamics in natural habitats. In the absence of significant natural enemy impacts during the growing season, lower densities of *E. elegantula* in more diverse landscapes are possibly the result of predation of overwintering adults. While a majority of biological control studies focus on dynamics during the growing season, it would be interesting to know more about natural enemy impact on pests during the overwintering period. Finally, evidence from previous studies has indicated that cover crops may require further management in order to force natural enemy movement into the crop canopy. As such, mark-recapture trials to evaluate natural enemy movement after mowing cover crops could provide useful information.

Implications of the Research

The use of on-farm habitat diversification to enhance biological control of pests has a practical and theoretical appeal to growers, consumers, regulators and scientists alike. This is evident in federal programs such as the Environmental Quality Incentives Program (EQIP 1996) that subsidizes growers to restore non-crop habitat on their farms, the marketing of “insectary

blends" of annual flowers by many of the major seed houses, and the wide variety of growers who experiment with them. Given their aesthetic value, flowering cover crops in particular are appealing for use in a crop like wine grapes where consumers regularly visit the winery and look at the vineyard itself. Consumers would probably even pay more for wine that was produced in a vineyard that had reduced pesticide applications by using flowering cover crops to enhance biological control of pests.

Yet there is a great distance between theory and reality and it is our role as agroecologists to critically evaluate the various theories we propose, regardless of how badly we want to see them succeed. After all of the years of hard work to develop and establish the use of flowering cover crops in vineyards, their inability to enhance biological control is certainly disappointing. But it also must be acknowledged that the establishment and management of flowering summer cover crops does require extra labor, fuel and material costs for growers and these are annual recurring costs since the flowers must be re-sown each fall. If these practices are not actually enhancing biological control, then knowledge of this is all the better for growers who would otherwise be wasting their time and money trying to maintain stands of flowering cover crops every year. To know that these flowers do not enhance biological control is the first step in moving towards other habitat management practices that do enhance biological control.

With that in mind, the area and composition of natural habitats that surround vineyards was found to significantly influence natural enemy populations and biological control of *E. elegantula*. This is encouraging and these findings can hopefully contribute to the development of regional habitat restoration and management programs. At present, programs like EQIP function on an individual, grower-by-grower approach, but programs like this will need to be modified in order to promote cooperation amongst multiple land owners in order to restore habitat diversity at the landscape scale. The need to increase habitat diversity in agriculture is still there, but the spatial at which this occurs may need to be adjusted as we begin to learn more about how crops, pests and their natural enemies interact across the greater agricultural landscape.

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