Title

Landscape and farm management effects on Ichneumonidae (Hymenoptera) diversity and parasitism of pests in organic vegetable production

Author

Bothwell, Sara G.

Publication Date

2012

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

LANDSCAPE AND FARM MANAGEMENT EFFECTS ON ICHNEUMONIDAE (HYMENOPTERA) DIVERSITY AND PARASITISM OF PESTS IN ORGANIC VEGETABLE PRODUCTION

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY in
ENVIRONMENTAL STUDIES

By

Sara G. Bothwell

September 2012

The Dissertation of Sara G. Bothwell
is approved:

Professor Deborah K Letourneau, Chair

Professor Gregory S. Gilbert

Professor Margaret FitzSimmons

Tyrus Miller
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Sara G. Bothwell

LANDSCAPE AND FARM MANAGEMENT EFFECTS ON ICHNEUMONIDAE (HYMENOPTERA) DIVERSITY AND PARASITISM OF PESTS IN ORGANIC VEGETABLE PRODUCTION

Land conversion and agricultural intensification reduce both on-farm and near-farm non-crop habitat for arthropod biodiversity, with potentially detrimental consequences for biological control of crop pests. The diversity of ichneumonid wasps, a large family of parasitoids, was sampled over three years and parasitism of two insect pests was measured in annual vegetable farms the following year; management practices were described and vegetation and landuse cover within 1.5Km were measured for each farm. Ichneumonidae species richness was positively associated with landscape-scale vegetative cover and field-scale crop diversity, but not with landscape-scale vegetation diversity; subfamily responses to both landscape vegetation classes and crop diversity varied. Species richness within Campopleginae and Cryptinae were positively associated with perennial vegetation and negatively associated with annual cropland, whereas diplazontine richness was positively associated with grasslands and negatively associated with freshwater. *Baccharis* shrubs and annual crop cover best explain the distribution of ichneumonid species, regardless of subfamily. Three ichneumonid and two braconid wasp species and tachinid flies parasitized *Trichoplusia ni* larvae, but major mortality was due to

Hyposoter exiguae (Ichneumonidae) in May and *Microplitis alaskensis* (Braconidae) in September. Spring parasitism rates were positively associated with annual crop and grassland cover—an opposite pattern to the abundance and species richness of the Ichneumonidae samples. *T. ni* parasitism in fall was positively associated with grassland cover, pest control intensity, and decreasing tillage, not perennial vegetation cover. Parasitism of *Brevicoryne brassicae* was not associated with landscape vegetation or with farm management. Although greater on-farm crop diversity and perennial vegetation conservation in cropland-dominated landscapes were associated with greater richness of Ichneumonidae, neither perennial vegetation nor wasp richness was associated with high parasitism rates of sentinel caterpillars or aphids in the following year. These results suggest that elements of the landscape mosaic are needed to support diverse communities of natural enemies, but pest control services do not necessarily map on to patterns of arthropod diversity. Over the long term, a more diverse community may provide "insurance" against pest outbreaks if a dominant parasitoid is lost, but areas of overlap between biodiversity conservation and agricultural goals must be assessed critically.

for Michael and Roger

and

for my dad, Dr. Alfred L.M. Bothwell

ACKNOWLEDGMENTS

I am grateful for support from many people on this journey.

My adviser, Deborah Letourneau, guided my entomological education as well as this dissertation. The HIPP research group (D. Letourneau, Carol Shennan, Tara Pisani Gareau and myself) worked as a team in the development of this project. D. Letourneau, along with my other committee members, Greg Gilbert, Nicholas Mills, and Margaret FitzSimmons, provided invaluable counsel and feedback.

Brian Fulfrost helped plan and manage the GIS component. Robert Kula and N. Mills identified wasp species. Pete Raimondi assisted with the BIO-ENV analysis in chapter one. Many students assisted with field and laboratory work: Katherine Long, Joanna Heraty, Joel Velasco, Tobin Woodley, Tony Laidig, and Dylan Neubauer. Greenhouse staff (Jim Velzey and Denise Polk) and ENVS Department staff helped keep very busy field seasons running smoothly.

I owe a great debt to all the farmers/growers who allowed me access to their fields, along with my traps, caterpillars, and aphids. They helped this research succeed in the midst of their needs to till, irrigate, and harvest. Thanks to Phil, Amy, Ramy, Steve, Brendan, Judy, Marc, Mark, Jamie, Maria Luz, Andy, John, Jeff P., Jeff L., Tim V., Dennis, Tom, Jim, Dean, Joe, Jim, Tim C., Patrick, Dick, Tom & Laurie, Nibby, Benny, and to Jeff Young, who is missed.

This research was financially supported by USDA-NRI grant #2005-0288 and UCSC STEPS Institute, CASFS, Environmental Studies Department, and Women's league.

I am grateful to my ENVS cohort: Tara, Katie, Barbara, Alex, Aaron, Ben, Mint, Hilary, and Dustin, and to Joy Hagen –resources, collaborators, and friends.

And to my family: my mother, Sallye, for always asking how my work was going, Peter for asking me to talk through all the details, my father, Alfred, for understanding the journey I have been on and especially for two epic days in the field together in 2005, my sister, Laura, for wanting to talk about other things, and my son Roger for being the most gratifying kind of distraction.

Finally, I am grateful to Michael, who not only helped in the greenhouse and in the field, but also kept things sane on the home front and kept me laughing.

INTRODUCTION

Land conversion and increasing intensity of land use have had negative impacts on global biodiversity (Green et al. 2005). Resources for biodiversity conservation are limited, leading conservationist to form practical partnerships with other conservation goals, such as conservation of ecological services, where overlapping opportunities exist (Balvanera et al. 2001). These opportunities have been limited, in part, by knowledge gaps regarding conservation of ecological services, although research has been closing these gaps for several services (Chan et al. 2006). The ecological service of biological control of agricultural insect pests by arthropod natural enemies involves a diverse and often complex array of interactions. One research facet has been examining the relationship between enemy diversity and biological control of arthropod pests. Overall, greater natural enemy diversity tends to yield greater pest control (Chaplin-Kramer et al. 2011, Letourneau et al. 2011). Our ability to identify clear overlaps between biodiversity and pest control conservation is limited by the importance of enemy species identity, rather than generic enemy diversity alone, and whether those two groups have common resource needs. Understanding the habitat requirements for conserving both natural enemy diversity and pest control is critical for identifying where positive overlaps or trade-offs occur, and can lead to more effective policy recommendations (Balvanera et al. 2001). Agricultural landscapes have gained recent attention both for restoring noncrop vegetation to conserve both biodiversity and ecological functions, such as water filtration and soil retention (AWQA 2008, CAFF 2010), but also for vegetation removal regulations because of food safety concern associated with wildlife (Beretti and Stuart 2008, Sutherland et al. 2012). Understanding how agricultural landscape features affect both insect natural enemy diversity and pest control is an important part of this policy conversation. In this dissertation, I investigate what habitat factors are associated with conservation of the parasitic wasp family Ichneumonidae and parasitism of two pest species in agricultural landscapes, and examine differences between them.

Intensification of agricultural landuse over the past 50 years has resulted in reduction or elimination of on- and near-farm noncrop vegetation (Merriam 1988) that is important habitat for native fauna (CAFF 2010). Many parasitic hymenoptera benefit from floral resources and require undisturbed areas during juvenile developmental stages. Thus proximity, amount, and variety of vegetation in the landscapes in which farms are embedded—particularly for annual cropping systems—may provide support for local wasp communities that are able to commute between resources and recolonize fields between crop cycles. The hymenopteran family Ichneumonidae is highly diverse and of conservation interest by farmers because of its potential to assist in insect pest control. In chapter one, I examine the relationship between farm management intensity, landscape scale factors, and Ichneumonidae within organic vegetable production in the central coast region of California. To do this, I measured three farm management variables that affect insect communities: crop diversity, insecticide use, and tillage frequency, characterized numerous vegetation and landuse classes within landscapes surrounding farms, and collected morphospecies richness and abundance data of Ichneumonidae sampled within the middle of production fields. I test which landscape- and farm-scale factors are positively associated with the abundance and species richness of this diverse family, and with three subfamilies that utilize different host taxa. Additionally, I test whether particular landscape features are associated with clusters of morphospecies, regardless of subfamily. These tests can help identify farm management practices and vegetation conservation or restoration targeted for ichneumonid conservation.

Prior research has indicated a positive relationship exists between landscape scale noncrop vegetation and pest suppression within crop fields (Bianchi et al. 2006). However, most studies have focused on predatory rather than parasitic interaction, in which there appears to be more variability in response. In chapter two, I report on the results of two sentinel pest experiments, designed to detect parasitism of agricultural crop pests. Using the same landscape and farm management approach from chapter one, I tested which landscape- and farm-scale factors are positively associated with parasitism of the cabbage looper caterpillar *Trichoplusia ni* and the cabbage aphid *Brevicoryne brassicae*. One ichneumonid species, *Hyposoter exiguae*, was responsible for much of the *T. ni* parasitism I measured. Parasitism of *T. ni*, including by *H. exiguae*, displayed opposite relational patterns to landscape-scale factors than did Ichneumonidae abundance and species richness patterns reported in chapter 1.

A relationship between Ichneumonidae and control of insect pests is assumed by local organic farmers, in part because of very general statements about the family in agricultural extension material (UCIPM 2007). While some species, such as *H. exiguae*, are documented enemies of pest insects, Ichneumonidae is a highly diverse taxon and host taxon use is often species-specific (Shaw 2006). In chapter three, I examine the criteria for selecting ecological service indicator taxa, the relationship between natural enemy diversity and ecological service provision, and provide a limited test of Ichneumonidae as an indicator for biological control service. This test is limited by use of only one sentinel species parasitized by Ichneumonidae in one year. I suggest a more robust method of testing whether Ichneumonidae can serve as an indicator. Ichneumonidae abundance, in particular, would be a practical evaluative tool for farmers and pest control advisers. Clearly evaluating whether a relationship exists between Ichneumonidae species richness and biological control services could play a role in the ongoing debate over vegetation restoration versus removal on central coast farmland.

CHAPTER 1

ICHNEUMONIDAE (HYMENOPTERA) AND SUBFAMILY DIVERSITY VARY IN RELATION TO LANDSCAPE AND FARM MANAGEMENT FACTORS

Abstract

Agricultural intensification has reduced both on-farm and near-farm habitat for arthropod biodiversity. Ichneumonid wasps may be conserved through landscape-scale vegetative refugia or less disruptive farm management practices. We measured ichneumonid diversity on annual vegetable farms in the central coast of California, where farming landscapes range from simple to complex and farming intensity varies. Ichneumonid species richness was positively associated with cover of noncrop vegetation in the landscape, but not with the diversity (richness) of vegetation classes. Abundance and species richness of Ichneumonidae and three subfamilies—Campopleginae, Diplazontinae, and Cryptinae—were all positively associated with crop diversity in farm fields, but subfamily responses to landscape vegetation classes varied. Campoplegine and cryptine richness were positively associated with noncrop perennial vegetation cover (specifically *Baccharis* shrubs), and negatively associated with annual cropland. In contrast, Diplazontine richness was positively associated with grasslands and negatively associated with freshwater cover. A BIO-ENV relate identified *Baccharis* (positive association) and annual crop cover (negative association) as best explaining the distribution of ichneumonid species, regardless of subfamily. Greater crop diversity at the farm level and conserving perennial

vegetation to annual crop-dominated landscapes can help conserve Ichneumonidae in this region, but different management may be required to conserve the right balance of ichneumonid species for biological pest control.

Introduction

Agricultural land has become more intensively managed over the past 50 years and near-farm remnant vegetation has been reduced (Merriam 1988) resulting in lower on-farm faunal diversity (Green et al. 2005). This reduction in diversity may also lead to loss of ecological services, particularly pollination services provided by bees (Kremen et al. 2007) and pest regulation provided by predatory and parasitic insects (Letourneau et al. 2009). Restoration of noncrop vegetation on farms and conservation of remnants of semi-natural vegetation have been promoted to improve habitat for native fauna and the services they provide (CAFF 2010) and to reduce surface water pollution (AWQA 2008). However, an outbreak of *Escherichia coli* O157-H7 in vegetable crops has sparked controversy and increased pressure to remove noncrop vegetation that may also harbor wildlife capable of carrying the bacteria from the surrounding landscape into the field (Beretti and Stuart 2008, Sutherland et al. 2012). Understanding how agricultural landscape intensification affects faunal diversity is critical to minimizing ecological service losses while protecting food safety.

Stable habitat (Southwood 1977, Tscharntke et al. 2007) and plant diversity (Landis et al. 2005) are important to maintaining natural enemy communities. There are fewer demonstrated cases of successful biological control in annual cropping systems than in perennial ones (Wiedenmann and Smith 1997, Letourneau and Altieri 1999), in part because the frequency and intensity of disturbance forces natural enemies into a pattern of "cyclic recolonization" from off-farm refugia (Wissinger 1997). Combined with the exclusion of floral resources, important for the longevity and fecundity of many parasitic wasp species (Baggen and Gurr 1998, Lee et al. 2004, Araj et al. 2008), intensive annual cropping practices require natural enemies to "commute" between spatially segregated resources (Jervis et al. 1993). For highly mobile taxa, like parasitic Hymenoptera that can disperse on the scale of kilometers to seek hosts (van Nouhuys and Hanski 2002), noncrop vegetation patches with 0.5 to two kilometers from farms can support local natural enemy communities (Thies et al. 2005) and their ability to control agricultural pest populations (Tscharntke et al. 2007).

Evidence from a variety of natural enemy taxa supports a general relationship between greater noncrop vegetation cover and species richness (Bianchi et al. 2006, Chaplin-Kramer et al. 2011), but there exist only a few tests regarding parasitic wasp diversity (Menalled et al. 1999, Menalled et al. 2003, Vollhardt et al. 2008, Bennett and Gratton 2012). The abundance of seven parasitic Hymenopteran families, including Braconidae and Ichneumonidae, was positively associated with increasing vegetation along an urban-rural gradient (Bennett and Gratton 2012). Menalled et al. (1999) found that total parasitoid abundance (six ichneumonid, braconid, and eulophid wasp species) was positively associated with landscape complexity in only one of three agricultural study regions, though this pattern was inconsistent across years (Menalled et al. 2003). Vollhardt et al. (2008), on the other hand, found no difference in the species richness of braconid aphid parasitoids captured in wheat fields embedded in simple versus complex landscapes.

Theoretically, the richness of vegetation classes (number of distinct vegetation types) should influence the diversity of parasitic wasps through the provision of a greater variety of host species (herbivorous insects) and floral resources (nectar sources) (Root 1973). Correlations between species richness of two ichneumonid subfamilies, Pimpinae and Rhyssinae, and Amazonian plant species richness was attributed to host use (Saaksjarvi et al. 2006). Generalist hymenopteran parasitoids of North American agricultural pests frequently use alternative host species that feed on trees and shrubs whereas the alternative hosts of specialist parasitoids' predominantly feed on shrubs and herbaceous weeds (Marino et al. 2006). Similarly, mixed-age Japanese forests likely support greater species richness of Braconidae because of greater host diversity, whereas young forests provide abundant herbivore hosts and old-growth forests provide detritivore hosts (Maleque et al. 2010). Fraser et al. (2007) determined that species richness of three of four ichneumonid subfamilies was positively associated with tree species richness in English forests. There are fewer examinations of the role of floral resource diversity on parasitoid communities. In an urbanized environment, species richness of concurrently flowering species was positively associated with parasitic wasp abundance, but not with the richness of parasitic families. Variation in floral morphology affects whether particular wasp species can access available nectar (Vattala et al. 2006). Additionally, variation in bloom period among plant species can provide temporal stability of floral resources (Earnshaw 2004). Thus landscapes with diverse non-crop vegetation in the landscape may support greater parasitoid diversity than less diverse landscapes with similar amount of non-crop cover.

A mosaic landscape perspective, in which multiple types of vegetation patches exist, allows weighing of their relative contributions to parasitic wasp communities. However, agricultural fields often are situated amidst landscape patches converted to nonagricultural purposes, including high speed roadways, which cause significant mortality in flying insect taxa like Odonata (Soluk et al. 2011) and Lepidoptera (Rao and Girish 2007). In addition, rural (i.e. isolated homesteads), residential, commercial and industrial land use in agricultural regions represent decreasing and homogenizing vegetative and increasing impervious cover, thus potentially decreasing resource availability and diversity. Increasing impervious cover is associated with decreasing parasitoid family richness (Bennett and Gratton 2012). A mosaic landscape perspective allows for investigation of particular land uses as well as vegetation types.

Less intensive farm management practices may mediate the effect of landscape-scale resource loss. Tillage frequency (Wissinger 1997), the scale of individual harvests (a few rows versus an entire field), and pesticide applications (Ohnesorg et al. 2009, Geiger et al. 2010) determine degree of disturbance within the local plant-insect community. Crop diversity, through spatial and temporal polycultures, can be manipulated to enhance local natural enemy communities (Altieri and Letourneau 1982, Letourneau et al. 2011). Holzschuh et al. (2010) determined that conventional (more intensive) farm management supports fewer predatory wasp species than does organic (less intensive) management, and that percent of noncrop vegetation in surrounding landscapes has a larger positive impact on wasp species richness in conventional fields. Overall, less intensive management benefits plant and animal species richness, but only in simpler landscapes, not in more complex ones (Batary et al. 2011). Thus on-farm and landscape-scale influences on species richness must be examined in concert.

Ichneumonidae includes an estimated 60,000 species of natural enemy wasps worldwide (Wahl and Sharkey 1993). This diversity may be related to host-specificity (Shaw 2006). As a family, Ichneumonidae attack a broad array of arthropod taxa, but with host taxon segregation among some subfamilies and highly specialization at the species level (Wahl and Sharkey 1993). For example, many Campopleginae use lepidopteran hosts, including known agricultural pests, whereas the Diplazontinae oviposit in predatory Syrphidae (Diptera) and thus may interfere with biological control of agricultural pests. Cryptinae is a species rich, but not well-studied group. Because there are sizeable gaps in knowledge of distributions, host species, and physical habitat requirements among Ichneumonidae (Shaw 2006), our ability to plan for their conservation in dynamic landscapes is limited (Gaasch et al. 1998).

In this study, we tested the hypothesis that the abundance and species richness of ichneumonid parasitoids visiting annual crop fields is positively associated with noncrop vegetation cover and vegetation richness in agricultural landscapes, and compared whether subfamilies that use different host taxa vary in response to particular landscape features or farm management factors. Specifically, we hypothesized that species richness is positively associated with landscape scale vegetative richness, mixtures of annual and perennial vegetation types, and in-field crop diversity but negatively associated with more intensely developed land uses and the intensity of disturbance from tillage events and pesticide applications. Additionally, we tested whether some species, independent of subfamily taxon displayed similar associations with landscape features. To test these hypotheses, we sampled Ichneumonidae within production farm fields, quantified management practices that affect insect populations, and characterized the landscape mosaics around farms that represent the range of organic vegetable production in the central coast region.

Methods

Study region and research sites

The central coast region of California consists of a mosaic of natural vegetation, such as wetlands, chaparral, oak woodlands, coniferous forest, and coastal prairies, as well as farming operations and urban development. Its mild Mediterranean climate supports vegetable production year round. Most of the approximately 450 mm average annual precipitation (NCDC 2009) occurs between October and April, with crops irrigated during the dry May through September months. Annual cropping systems dominate agriculture in the three counties included in this study (Santa Cruz, Monterey, and San Benito), producing 16% of the national and 28% of the Californian market value for vegetables, melons, potatoes, and sweet potatoes with a disproportionately high acreage in organic production (~10% of California organic acres harvested within less than 4% of total California acres) in comparison to the rest of the United States; California contains 62% of national organic vegetable production acres (CCOF 2008, USDA 2009). Of approximately 50 certified organic vegetable growers in Santa Cruz, Monterey and San Benito counties, 25 agreed to host research on 34 certified organic farm fields (hereafter called sites) that were separated by at least 1 km, and within a one-hour driving distance from the University of California, Santa Cruz. The northern-most site (37°06’33.83”N, 122°16’20.06”W) was 60 kilometers north of the southern-most site (36°32’21.30”N, 121°51’45.24”W) and 80 kilometers west of the eastern-most site (36°51’74”N, 121°18’31.42”W) (Fig. 1.1). This geographic distribution encompasses coastal areas and inland valleys, which vary in average temperatures, and encompasses the range from simple to complex mosaic landscapes.

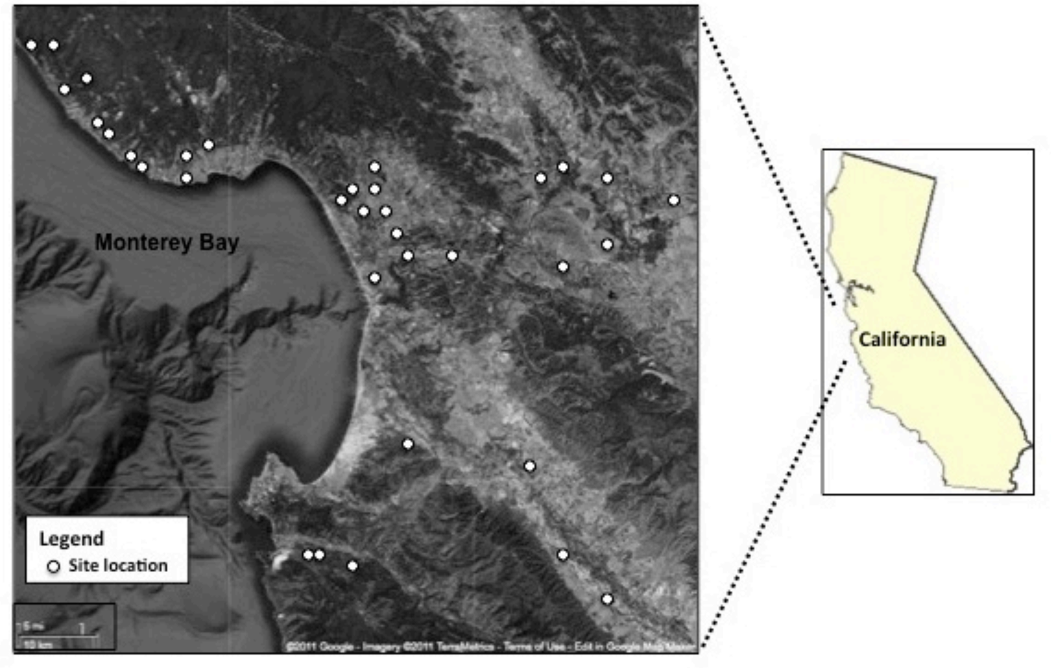


Figure 1.1. The geographical distribution of 34 farms fields used as research sites in this study, within the central coast region of California.

Landscape and farm management characterization

In a geographic information system (GIS), we designated 0.5 km (small) and 1.5 km (large) radius circular landscape areas (0.785 km^2 and 7.07 km^2, respectively) around the center point of each site (Fig. 1.2) to measure small and large landscape-scale features; these distances were based on prior multi-scale studies of parasitic wasp movement in agricultural landscapes (Letourneau and Goldstein 2001, van Nouhuys and Hanski 2002, Thies et al. 2003) and to the importance of considering different scales among species (Steffan-Dewenter 2002). We manually digitized and attributed polygons with one of nine land-use (e.g., annual or perennial cropland, paved or gravel roads, industrial and residential areas) or forty-one vegetation classes (e.g., conifer, *Quercus*, or *Eucalyptus* forest, *Salix* or marsh riparian vegetation, *Baccharis* and *Salvia* shrubland, mixed forbs or grassland) determined ad hoc, based on our ability to characterize them (e.g. various coniferous trees were not reliably distinguishable). Vegetation mixes were denoted by dominant taxa in order of their prominence, such as oak-conifer, considering all taxa with greater than 10 percent coverage within the polygon; this yielded several 3-taxa vegetation classes. Ground-truthing for these categorizations of vegetation, which comprised field-based checks of 300 randomly selected points within the 34 digitized landscapes, showed a >89% accuracy rate. Subtle distinctions in hue and pattern characteristics, such as occur between *Quercus* and *Salix* designations, were the sources of identified attribution error. More detailed methods, the list of 50 distinct land-cover categories, and a description of our quality assessment process are located in Appendix 1. We used these data to generate percent land cover estimates for all cover types present in the 34 small (0.5km radius) and large (1.5km radius) landscapes (A1).

To reduce this large number of dependent variables, some of which covaried, we conducted Principle Component Analyses (PCA). Vegetation and landuse types present in very few landscapes (e.g., "*Acacia*" was present in only two landscapes) or represented less than one percent of cover in any landscape (e.g. "*Baccharis*-grass" and "grass-forbs"), were grouped into larger categories based on dominant vegetation (e.g. "*Baccharis*" comprising *Baccharis* alone, *Baccharis*-grass, and *Baccharis*-hemlock classes) and/or broader relationships (grasslands, perennial vegetation, and noncrop vegetation), allowing us to include data from variables that otherwise would have been excluded to meet the assumptions of PCA. Additionally, we created a vegetation richness variable—the number of noncrop vegetation classes present in each landscape. Based on these adjustments, we included 17 classes in the large scale PCA and, separately, 15 classes for the small scale PCA.

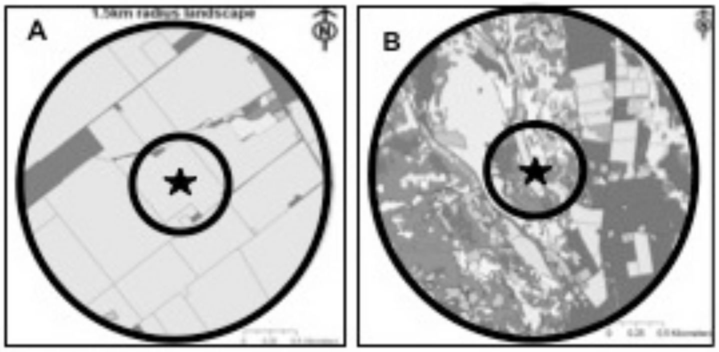


Figure 1.2. GIS characterizations of large 1.5km radius (outer circle) and small 0.5km radius (inner circle) landscapes based on the centerpoint (star) of organic vegetable farms ranging from relatively simple (A) to more complex (B) vegetation and landuses.

We measured three farm management factors that are known to influence resource availability for natural enemies: crop diversity, tillage, and pesticide application. Crop diversity values one through four were assigned in ascending order for monoculture, *Brassica* and *Lactuca* crops, two to three additional plant families, and more than four plant families, based on the average number of crops grown per field in 2004-2006. Tillage disturbance was counted as the number of crop transitions per year, when the entire vegetative structure of a field was disked into the soil before replanting. Pesticide use severity was calculated as a sum of all insecticide (USDA NOP allowed substances) applications or vacuuming multiplied by a weight based on the breadth and duration of action for each substance (weights: 0.25 = vacuum; 1 = soaps, oils, Bt; 2 = pyrethrum, spinosad). Weights were assigned based on whether they affect Hymenoptera directly (e.g. pyrethrum), only indirectly through host population reduction (e.g. Bt), or by the extreme frequency of their use (vacuuming).

Wasp sampling

To measure the diversity of Ichneumonidae visiting central coast farms, we collected 48-hour Malaise trap (BioQuip model 2875AG, 1.2 m wide x 2.13 m tall, with green netting) samples during September 2004 and May, July, and September of 2005 and 2006 in each site. Use of Malaise-style traps is an effective means of sampling Ichneumonidae (Darling and Packer 1988, Fraser et al. 2008) and allows collection of insects during flight, regardless of wind direction. Dark green traps (BioQuip model 2875AG), which work better than the standard white-top design in open, sunny conditions (Townes 1972), were erected at the center of each site, or if farming operations made the center unavailable, then in adjacent sections of the field within 50m of the center. Flexibility in sampling location was required due to overhead irrigation and mechanical cultivation timing, and changing crop type throughout the season. Communication with farm management minimized the likelihood that either a) a sample would be affected by these factors or b) a trap would impede their normal farm operations. Trapping positions were selected to keep crop type as consistent as possible across all farms with the following priority ranks: cole crops (*Brassica oleracea*), then lettuce (*Lactuca sativa*) varieties, and finally other vegetable crops.

Individual specimens were mounted, assigned a collection reference number, and labeled with acquisition data. We identified Ichneumonidae to subfamily based on Wahl and Sharkey (1993). Specimens within each subfamily were grouped into morphologically distinct "morphospecies" (Oliver and Beattie 1996, Skillen et al. 2000); morphospecies were based on available generic keys (e.g. Townes 1969) in consultation with Dr. Nicholas Mills (*personal communications*), and our detailed descriptions to help distinguish similar morphospecies (A2). We recorded the abundance of each morphospecies per sample and generated the species richness and abundance values per sample for Ichneumonidae as well as for the numerically dominant subfamilies. Specimens of morphospecies found at least 12 times were sent to the USDA Systematic Entomology Lab/Smithsonian Institution in Washington, D.C. for identification.

Data analysis

To test whether there is a relationship between the ichneumonid community and landscape-scale vegetation, we conducted a regression of the cumulative abundance and species richness of Ichneumonidae against the percent of landscape areas under noncrop vegetation at both the 1.5km and 0.5km landscape scales. To test whether Ichneumonidae or key subfamilies were associated with particular vegetation types, we conducted multiple regressions in PC-SAS version 9.2 (SAS 2003), using the first five principle landscape components and the three management factors (a suite of 8 variables), and repeated these analyses for both 1.5km and 0.5km landscape scales. We used AIC values (Beal 2005) to select models that best describe the distribution of ichneumonid abundance and species richness. Models with AIC values at least 1-integer lower than alternative models were considered to best explain the distribution of Ichneumonidae; models including fewer variables were selected for tests yielding equivalent alternative models (<1-integer difference in AIC scores). In the case where highly complex models yielded the lowest AIC scores, selection was based only on models containing four or fewer variables. Landscape variables that were strongly loaded (>0.35) on significant components were considered to be explanatory. Additional parallel multiple regressions were conducted to examine how the abundance and species richness of subfamilies of differing host taxon use—in particular the Campopleginae, Cryptinae, and Diplazontinae—might differentially relate to landscape context, using the same landscape component and farm management suite.

To identify whether particular wasp species were similarly distributed across sites, independently of subfamily taxon, we conducted a cluster analysis by building a Bray-Curtis similarity matrix for quarter-root transformed mean abundance data of the seven sampling periods. To investigate whether species groupings are associated with particular vegetation or landuse classes, we conducted a BIO-ENV Relate (Clarke and Warwick 1994) between normalized landscape data and a species abundance matrix in PRIMER 6. To then identify which species in particular were driving identified associations, we conducted a PCA of the species abundance data, using a varimax rotation to limit the number of factors identified. Using components that explained at least 5% of the species variation, we conducted Pearson's correlations to test whether these components were associated with the vegetation and landuse classes identified through BIO-ENV. Explanatory species were identified through their eigenvalue loadings on significant components.

Results

Farm management and landscape complexity

Non-crop vegetation cover across the 34 landscapes included in this study ranged from 2% to 97% (1.5km scale) and from 1% to 89% (0.5km scale). At the 1.5km landscape scale, noncrop vegetation was composed primarily of coniferous forest (mean = 19%), grassland (16%) and California live oak forest (9%) while at the 0.5km landscape scale, noncrop vegetation area was primarily grassland (15%), coniferous forest (14%), and residential areas (11%). The landscapes ranged from intensively managed agricultural landscapes (Fig. 1.2a), to remote farms surrounded by a few vegetation classes, to complex mosaics including multiple vegetation and landuse classes (Fig. 1.2b). Vegetation and landuse classes that represented at least one percent cover (Table 1.1) were included in the PCAs. For a complete list of vegetation and land use classes by area for each site, see Appendix 1. PCAs of the vegetation and landuse variables yielded five explanatory components at both the 1.5km (LC1-5, explaining 75 percent of the variance) and 0.5km scales (SC1-5, 74 percent of variance) (Table 1.2). Farm size among the 34 sites ranged from 0.01 to 1 km^2, crop diversity from one to four (monoculture through polyculture including at least four plant families, mean = 2.6 ± 1.1SD), tillage frequency from one to four major events per year (mean = 2.6 ± 0.9SD), and pesticide severity from zero to 15 (ranging from no actions to scheduled vacuuming and insecticide applications, (mean = 1.4 ± 2.9SD). Pearson's correlation tests among pairs of landscape components and farm management factors yielded only one significant relationship: a negative association between crop diversity and pesticide use severity ($R^2 = 0.1799$, $p = 0.0139$).

Table 1.1. Percent vegetation and landuse class cover for 34 agricultural landscapes at both the larger (1.5km radius) and smaller (0.5km radius) landscape scales.

Variable	**Larger scale**		**Smaller scale**	
	Mean	**SD**	**Mean**	**SD**
Vegetation classes[1]				
annual crop	0.259	0.261	0.386	0.318
perennial crop	0.024	0.056	0.021	0.062
conifer	0.097	0.194	0.069	0.137
Baccharis	0.055	0.073	0.043	0.083
Eucalyptus[2]	0.010	0.014	0.009	0.019
freshwater[3]	0.010	0.147	0.013	0.022
grasslands	0.213	0.157	0.176	0.142
marsh[2]	0.013	0.029	0.009	0.023
Quercus	0.083	0.093	0.048	0.068
Salix	0.026	0.019	0.036	0.036
noncrop vegetation	0.522	0.246	0.421	0.282
perennial vegetation	0.310	0.247	0.247	0.224
vegetation richness[4]	8.79	3.39	6.12	3.18
Landuse classes				
paved road	0.015	0.014	0.017	0.021
commercial/industrial	0.034	0.038	0.043	0.085
residential	0.065	0.080	0.065	0.113
rural	0.008	0.014	0.013	0.018

[1] Only classes included in the PCAs are included in this table. Several vegetation categories and ocean cover were excluded due to absence in a majority of sites. Noncrop vegetation combines coverage of all vegetation classes, including those with low coverage (e.g. *Acer*, *Salvia*, coastal scrub, and others listed in Appendix 1). except for annual and perennial cropland . Perennial vegetation combines all perennial vegetation classes except for perennial cropland. [2] *Eucalyptus* and marsh classes were excluded for the 0.5km scale analysis because they were absent in a majority of sites. [3] Freshwater is not a class of vegetation but is a potentially important physical feature; it is included under “vegetation” classes in this table for simplicity. [4] Vegetation richness is a count of the number of vegetation classes within each landscape, not a percent cover measure.

Table 1.2. Strong loadings for 1.5km (LC1-5) and 0.5km (SC1-5) scale landscape PCA components by vegetation and landuse classes.

Component (% var explained)	**Landscape variable**	**Eigenvector loading (-/+)**
LC1 (26.12)	annual crop	0.4297
	Baccharis	-0.349
	noncrop vegetation	-0.4253
	perennial vegetation	-0.4274
LC2 (16.44)	*Eucalyptus*	0.3774
	paved road	0.3481
	commercial/industrial	0.3539
LC3 (14.62)	freshwater	-0.3892
	marsh	-0.3662
	Salix	-0.4607
	rural	-0.4876
LC4 (9.87)	freshwater	-0.4181
	perennial crop	0.4585
	grassland	0.4610
LC5 (8.31)	rural	0.3579
	grassland	-0.6073
SC1 (30.465)	annual crop	0.4297
	noncrop vegetation	-0.4334
	perennial vegetation	-0.412
SC2 (14.194)	conifer	-0.3927
	Baccharis	-0.3213
	residential	0.3748
	vegetative richness	0.3445
SC3 (11.907)	freshwater	-0.5972
	Salix	-0.4674
SC4 (9.233)	residential	-0.3754
	grassland	0.6163
SC5 (7.92)	commercial/industrial	0.6408

Ichneumonidae richness and abundance

Malaise trap samples from the 34 farms yielded 4700 ichneumonid wasps comprising 109 morphospecies (A2) belonging to 14 different subfamilies and attacking a diverse array of host orders (Table 1.3). The mean ichneumonid abundance per site per 48-hour sample was 24.8 (range: zero to 205, median: 11); the mean number of morphospecies was 7.8 (range: zero to 33, median: 7), distributed mostly (93%) among four subfamilies: Cryptinae (27%), Campopleginae (25%), Diplazontinae (23%), and Orthocentrinae (18%). Three morphospecies (*Diadegma* sp., *Stenomacrus* sp., and *Syrphoctonus* sp.) were by far the most common species in the samples (40% of total capture, collectively, Fig. 1.3) and represent natural enemies of Lepidoptera, likely mycetophagous Diptera, and Syrphidae (Diptera), respectively. Forty-nine species had fewer than 10 individuals, with 17 morphospecies represented by singletons. Sample sizes for subfamilies Campopleginae, Diplazontinae, and Cryptinae were sufficiently large and species rich to examine in relation to landscape and farm management factors.

Table 1.3. Ichneumonidae subfamilies and numerically abundant species collected by Malaise traps in 34 organic farms in 2005, 2006, and 2007.

Subfamily	**N mspp.**	**Abund**	**Host taxa**[1]	**Numerically dominant species (number, %of total capture)**[2]
Banchinae	11	87	Lep	
Campopleginae	13	1153	Lep	*Diadegma* sp. (680, 14.5), *Hyposoter exiguae* (98, 2.0), *Hyposoter* sp. 2 (94, 2.0)
Cryptinae (prev. Phygadeuontinae)	33	1276	Hol, Ara	Cryptinae sp. 1 (245, 5.2), Cryptinae sp. 21 (167, 3.6), Cryptinae sp. 24 (157, 3.3)
Cremastinae	3	3	Lep, Col	
Diplazontinae	14	1097	Dip	likely *Syrphoctonus* sp. (552, 11.7), *Sussaba* sp. (132, 2.8)
Ichneumoninae	10	50	Lep	
Labeninae	3	4	Col	
Mesochorinae	4	34	Hym, Lep	
Metopiinae	4	60	Lep	
Orthocentrinae	4	843	Dip	*Stenomacrus* sp. (662, 14.1), *Picrostigeus* sp. (170, 3.6)
Pimplinae	5	51	Lep, Ara	
Tersolichinae	1	1	Col, Sym	
Tryphoninae	2	37	Sym, Lep	
Xorinidae	1	1	Col, Sym	
unknown	-	3	-	
TOTAL	108	4700	-	

[1] Host orders: Col=Coleoptera, Dip=Diptera, Hym=Hymenoptera, Lep=Lepidoptera, Sym=Symphyta, Ara=Araneae, Hol=holometabolous insects. [2] Numerically dominant species=ten most highly abundant ichneumonid species trapped.

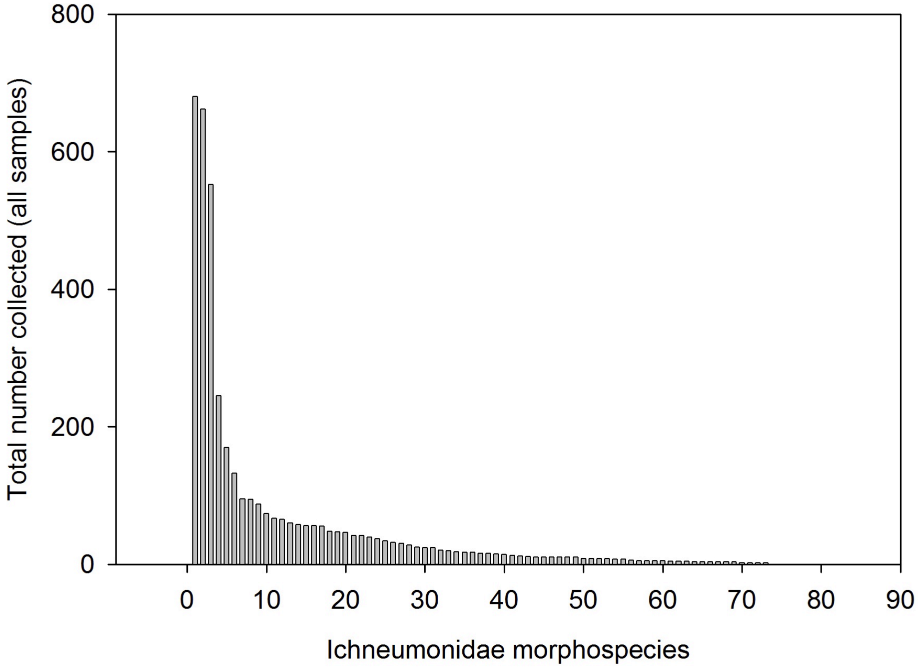


Figure 1.3. Rank abundance of ichneumonid morphospecies collected from Malaise traps

Associations between Ichneumonidae, and landscape complexity, and farm management

Ichneumonid species richness was positively associated with noncrop vegetation at the 0.5km scale (R^2 = 0.1256, p = 0.0504, Fig. 1.4a; NS at 1.5km scale R^2 =0.0094, p = 0.2874). This relationship was likely driven by Campopleginae, the species richness of which was positively correlated with noncrop vegetation cover (R^2 = 0.1727, p = 0.0201 at 1.5km; R^2 = 0.2166, p = 0.0083 at 0.5km) (Fig. 1.4b,c). Ichneumonid abundance, however, was unrelated to the percent of noncrop vegetation at either landscape scale (R^2 = 0.3918, p = 0.09112 at 1.5km scale, Fig. 1.4d; R^2 =

0.0084, p = 0.6231 at 0.5km scale). Ichneumonidae abundance was not associated with vegetation richness (R^2 =0.0014, p = 0.8393 at 1.5km; R^2 = 0.0055, p = 0.6903 at 0.5km) nor was species richness (R^2 = 0.082, p = 0.1187 at 1.5km, R^2 = 0.103, p = 0.0700 at 0.5km). Neither abundance nor species richness of Diplazontinae or Cryptinae was related to noncrop vegetation cover or richness.

Landscape variable-based PCAs yielded five explanatory components at both the large (LC 1-5) and small scales (SC 1-5). Multiple regressions to distinguish relative importance among vegetation types or farm management practices included five landscape components and three management (8 total) variables each at the two scales. Models selected were very similar at both scales, so we present results for the 1.5km scale only, except where differences exist. The most robust pattern detected was the positive relationship between crop diversity and wasp abundance and species richness—this farm management practice was present in nearly every significant model for Ichneumonidae and the subfamilies (Table 1.4, Fig. 1.5). The model selected for Diplazontinae abundance at the larger landscape scale alone did not include crop diversity, however at the smaller landscape scale, that was the only factor selected (Table 1.4). The other pattern consistent across multiple metrics was a negative association between LC1 and species richness of Ichneumonidae (Table 1.4, Fig. 1.6a), Campopleginae, and Cryptinae (Fig. 1.6b). LC1, with strong positive loadings of annual crop cover and negative loadings of perennial vegetation, especially *Baccharis* (Table 1.2), this negative relationship thus represents a negative association between our measures of wasp species richness and annual cropland cover but a positive relationship with perennial vegetation. At the 1.5km landscape scale, variation in Diplazontinae abundance was explained by LC4, representing a positive influence of grassland and perennial crop cover, and negative association with freshwater (Table 1.4). This association between Diplazontinae abundance and LC4 represents the single subfamily deviation from components of the family-level explanatory model. Meanwhile, the model explaining Ichneumonidae richness included a positive association with LC5 (strong negative loading of grasslands cover, Table 1.2), although this component did not contribute to the model explaining Ichneumonidae abundance (Table 1.4). Tillage intensity partially explained the abundance of Ichneumonidae and Campopleginae, in that no-till sites had lower abundances of these groups than did sites with mid-high levels of disturbance, and pesticide use severity was negatively associated with campoplegine richness (Table 1.4).

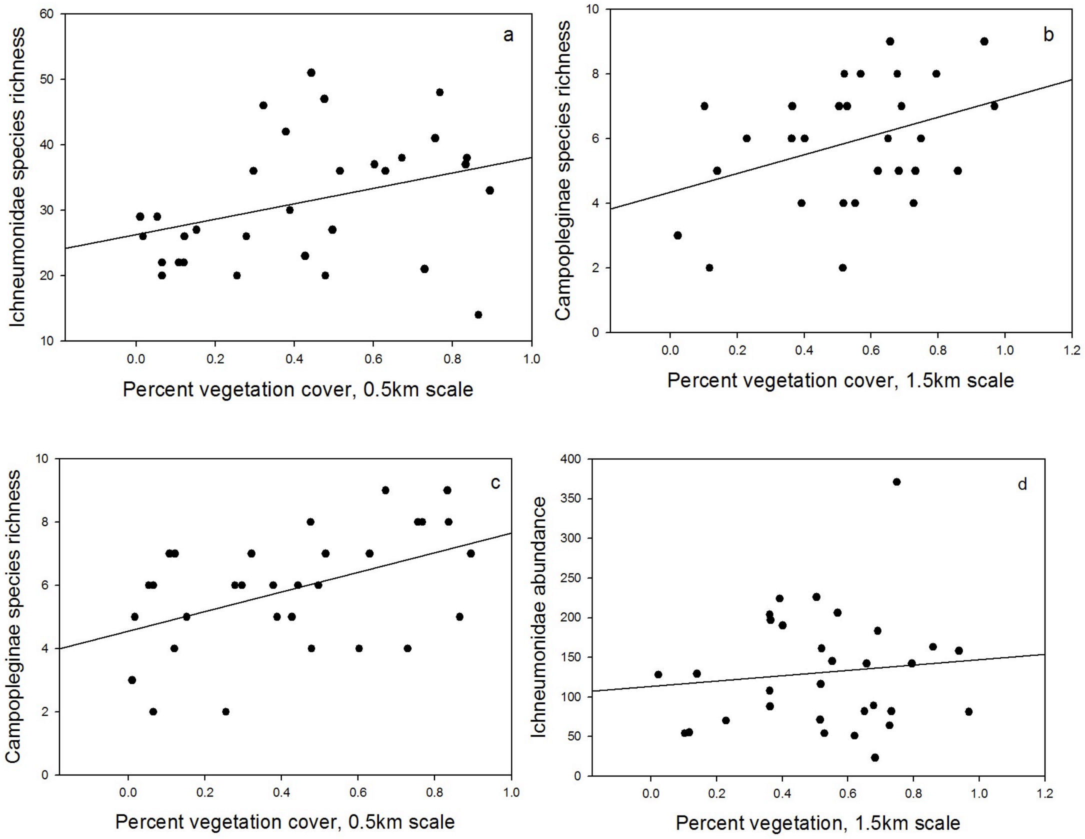


Figure 1.4. Relationships between species richness and percentage of noncrop vegetative cover for (a) Ichneumonidae at the 0.5km radius landscape scale, (b) Campopleginae at the 1.5km landscape scale, and (c) Campopleginae at the 0.5km landscape scale. Ichneumonidae abundance was not related to percent of noncrop vegetative cover (d).

Table 1.4. Multiple regression results for Ichneumonidae and key subfamilies. Abbreviations for farm management variables: crop diversity (crop div), tillage severity (till sev), and pesticide use severity (pest sev).

Community measure	**Coefficients & variables**	**df / F**	**p**	**R^2**
Ichneumonidae abundance	15.93 crop div, 33.49 till sev	2, 28 / 6.07	0.0065	0.4018
Ichneumonidae richness	5.05 crop div, -1.28 LC1, 2.11 LC5	3, 27 / 8.02	0.006	0.4926
Campopleginae abundance	6.26 crop div, 6.00 till sev	2, 28 / 5.66	0.0086	0.3424
Campopleginae richness	0.62 crop div, 0.43 till sev, -0.30 LC1	3, 27 / 5.04	0.0067	0.5762
Diplazontinae abundance	9.62 LC4 (1.5km scale) 10.85 crop div (0.5km scale)	1, 29 / 6.15 1, 29 / 5.33	0.0192 0.0283	0.2094 0.1023
Diplazontinae richness	1.22 crop div	1, 29 / 14.85	0.0006	0.3016
Cryptinae abundance	9.46 crop div, -2.41 LC1	2, 28 / 6.95	0.0035	0.2800
Cryptinae richness	2.07 crop div, -0.59 LC1	2, 28 / 6.37	0.0053	0.3127

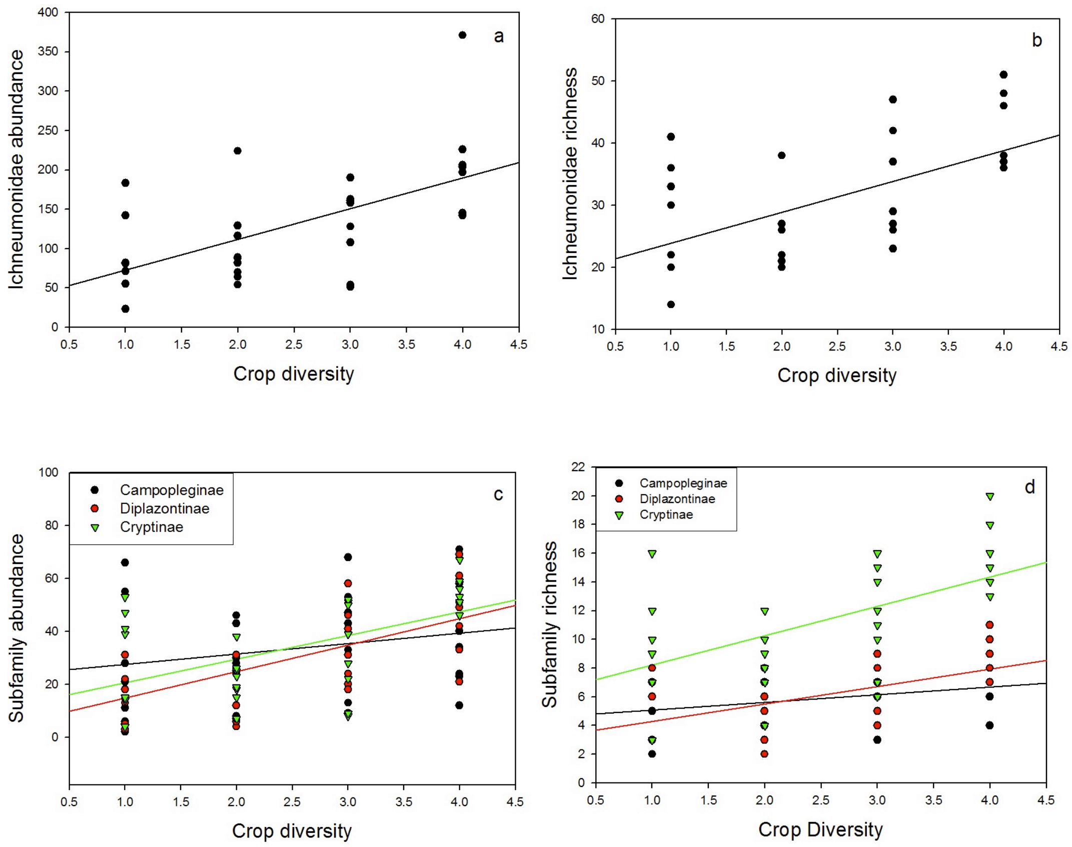


Figure 1.5. The consistently positive relationship between crop diversity and wasp samples: Ichneumonidae (a) abundance and (b) species richness, and subfamily (c) abundances, and (d) species richness.

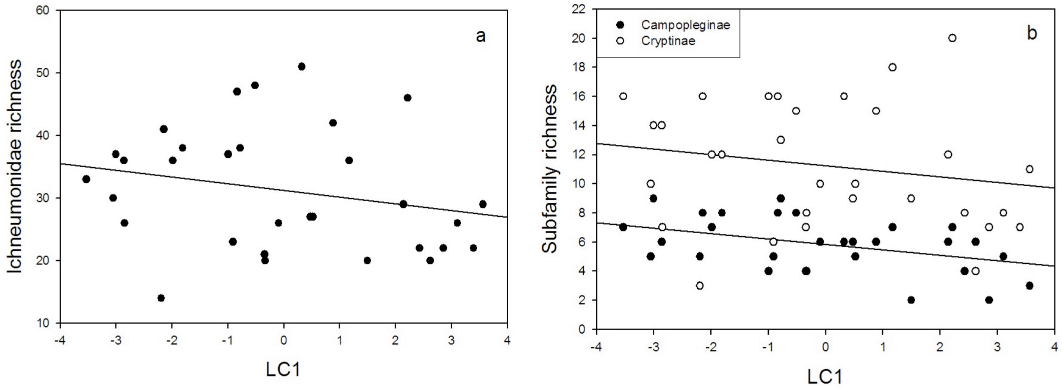


Figure 1.6. The negative relationship between species richness and 1.5km scale component one (LC1: +annual crop/-noncrop, perennial, and *Baccharis* vegetation cover) for (a) Ichneumonidae and (b) subfamilies Campopleginae and Cryptinae.

In our investigation of species-level associations separate from taxonomic groups, Bray-Curtis similarity matrixes yielded no site clusters based on species similarity. From BIO-ENV analysis, identifying landscape variables that best explain distribution similarities within the species abundance matrix, at the 0.5km scale, the simplest best fit model included three landscape classes—*Baccharis*, annual crop, and rural (rho = 0.227); at the 1.5km scale, the simplest best fit model included only *Baccharis* (rho = 0.210).

PCA of the normalized species abundance data yielded six axes that explained at least five percent of the variation in species distribution. Pearson's correlations to test whether these components were associated with the vegetation and landuse classes identified through BIO-ENV yielded few significant relationships, however (Table 1.5a). Surprisingly, *Baccharis* cover at the 1.5km scale was not associated with any of the components. Significant, but weak relationships between 0.5km scale *Baccharis* cover and components one (positive) ($R^2 = 0.104$, $p = 0.0623$) and two (negative) ($R^2 = 0.371$, $p = 0.0001$) were driven by strong values at both high (40%) and low (0%) cover sites (Fig. 1.7a-b). Among the farms included in this study, a coverage gap exists between 20 and 40 percent for *Baccharis* at the 0.5km landscape scale, which limits our ability to interpolate whether the sites driving these relationships are statistical outliers or part of a biologically meaningful trend. Thus we remain uncertain whether species that are strongly loaded on component two reflect an affinity for (negative loadings) or dissociation with (positive loadings) *Baccharis* cover (Table 1.5b). Annual crop cover at the 0.5km scale was positively associated with component three ($R^2 = 0.125$, $p = 0.0402$) and marginally negatively associated with component one ($R^2 = 0.087$, $p = 0.090$) (Fig. 1.7c-d), identifying nine species (Table 1.5b) that have a negative relationship with annual crop cover. None of the components was associated with 0.5km scale rural landuse. None of the species strongly loaded on components one, two, or three is among the top ten most abundant species captured in the samples.

Table 1.5a. Summary of simple regression results using significant species-based principle components.

	Species components					
Vegetation/landuse variable and scale	1		2		3	
	R^2	p	R^2	p	R^2	p
Bacccharis large	0.0011	0.2429	0.0644	0.1477	0.0203	0.4016
Baccharis small	0.1044	**0.0623**	0.3632	**0.0001**	0.0204	0.4196
annual crop small	0.0872	**0.0900**	0.0005	0.2969	0.1251	**0.0402**
rural small	0.0230	0.3276	0.0116	0.5435	0.0027	0.7624

Table 1.5b. Strong species loadings on PCA components significantly associated with key landscape variables. Morphospecies codes correspond to descriptions in Appendix 2.

Component	**Morphospecies**	**Eigenvector loadings**
1	DIP4 ICH3 MET3 PHY11A PIM1	0.2153 0.2293 0.2308 0.2014 0.2536
2	BAN2 CAM7 DIP2B ICH1 PHY8A	0.2069 -0.2177 -0.2296 0.2189 0.2020
3	CAM5 CAM6A DIP2A PHY7	-0.2274 -0.2216 -0.2504 -0.2266

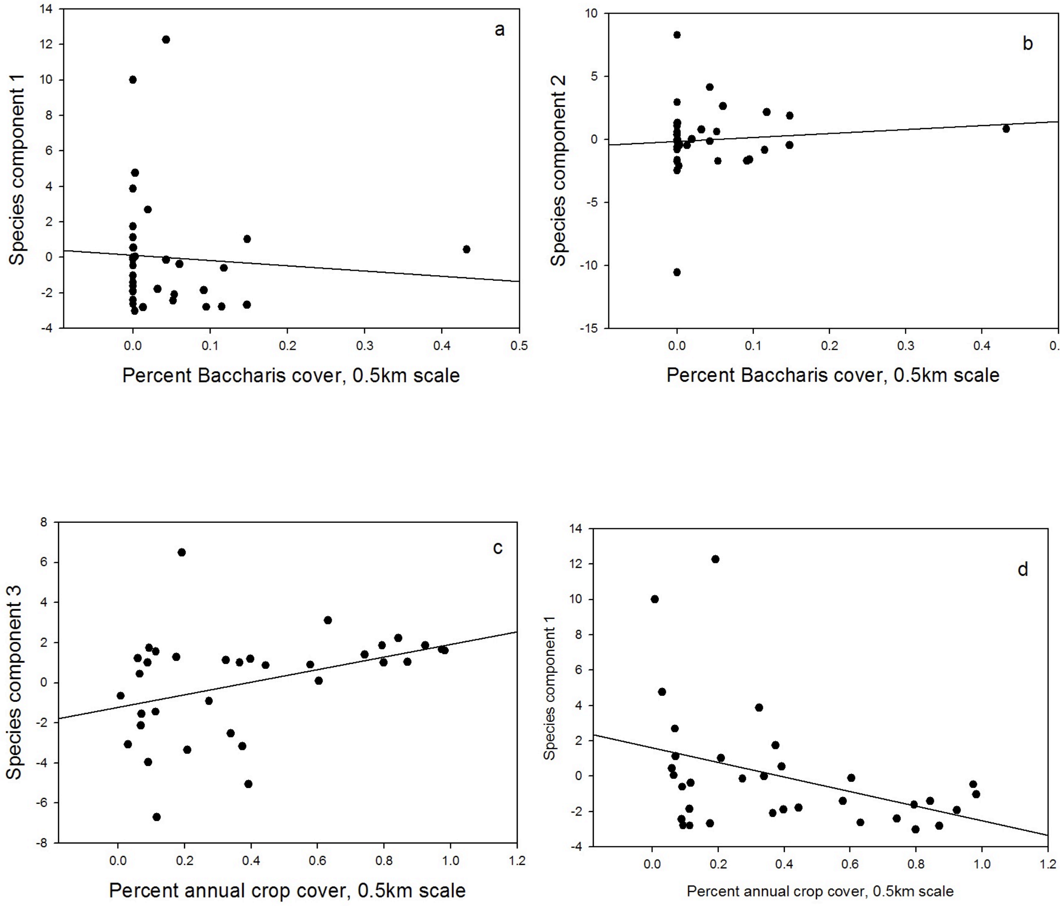


Figure 1.7. Relationships between principle species components and key vegetation types at the small (0.5km radius) landscape scale: (a) species component 1 and (b) species component 2 with *Baccharis* cover, (c) species component 3 and (d) species component 1 with annual crop cover.

Discussion

While theory and some evidence (Marino et al. 2006, Fraser et al. 2007) led us to hypothesize that we would find greater species richness of Ichneumonidae in landscapes containing both greater noncrop vegetative cover and greater vegetative diversity, we found a positive association for the former but not the latter. However, by examining family and subfamily-level associations with landscape mosaic components and farm management intensity, we were able to identify taxon-specific associations that illustrate why the presence of key vegetation categories contributes to Ichneumonidae conservation while vegetative diversity per se does not. Particular vegetation classes at both the smaller and larger landscape scales, in addition to farm management, were associated with each measure of ichneumonid diversity. Thus both on farm practices and multiple vegetation classes with the surrounding landscape are important to the support of ichneumonid diversity within the highly disturbed condition of annual vegetable farming.

Overall positive relationships between within-field crop diversity and wasp species richness and abundance suggests that crop fields with more plant families provide a broader suite of host species than do fields containing less diverse plant mixes or monocultures, thus attracting a greater variety of these relatively specialized parasitoids. In the central coast region, more diverse fields, containing different cultivars and ages of crops, tend to experience harvesting disturbance on the scale of a few rows or partial fields at a time. By contrast, monoculture fields typically are entirely harvested in one day, with no refugia left in the field. We speculate that a positive association between tillage disturbance and Ichneumonidae and Campopleginae abundance may reflect the success of the *Diadegma* species most frequently caught in our samples, which may specialize on quick recolonizing crop pests (Ehler and Miller 1978). The robust relationship between crop diversity and

Ichneumonidae within organic vegetable fields is important because local farmers are more able to adapt management practices than their surrounding landscapes, and is consistent with prior findings that less intensive agriculture supports greater (Letourneau et al. 2011). What differs from prior studies combining landscape and farm management factors is that we found crop diversity benefits wasp conservation across the range of landscape mosaics rather than finding a difference between simple versus complex landscapes (Batary et al. 2011). A paired simple-complex site study design would allow more explicit testing of that difference, however the geographic distribution of organic vegetable farms in central coast region of California does not facilitate such a design.

While Campopleginae and Cryptinae reflected the same association patterns as Ichneumonidae, the positive association between Diplazontinae abundance and grasslands cover (LC4) represents a deviation. As parasitoids of Syrphidae, important predators of aphids in these sites, large numbers of particular diplazontine species could potentially interfere with biological control. Landscape-scale studies of Syrphidae abundance (Werling et al. 2011) and species richness (Ricarte et al. 2011) indicate that grasslands are a less suitable habitat than are herbaceous or wooded vegetation, though mechanisms behind this pattern have not been identified. Investigating parasitism levels of Syrphidae in agricultural landscapes with high grassland cover would be an important extension of our result. Ichneumonid richness, on the other hand, was negatively associated with grassland cover (LC5). This result is surprising because California grasslands contain numerous flowering herbaceous species, including wild relatives of several vegetable crops, which should provide host insects and floral resources. For example, access to sugar extends adult longevity and increases female fecundity in many species, such as *Venturia canescens*, a campoplegine) (Eliopoulos and Stathas 2005). However, it may be that the seasonal drying of California grasslands results in a decline in those resources by our July and September sampling dates each year. Additionally summer midday temperatures in exposed areas are high enough to diminish the longevity of some Ichneumonidae (e.g. *Mastrus ridibundus*) (Devotto et al. 2010).

Associations between *Baccharis* alone and a subset of ichneumonid species as well as with campoplegine and cryptine species richness (their association with LC1) are not unexpected given documented relationships between some Ichneumonidae and this shrub. Tilden (1951) reared several ichneumonid species from herbivores collected on *Baccharis* and suggested that ichneumonid association with the plant may be primarily related to host use. Pisani Gareau and Shennan (2010) found a robust association of Ichneumonidae sampled from *Baccharis* hedgerow plants independent of bloom period and irrespective of plant sex, though they did not distinguish among ichneumonid taxa. Kido et al. (1981) found comparatively higher levels of parasitism and smaller infestations of the orange tortrix *Argyrotaenia citrana* (Fernald) in vineyards near wild *Baccharis* plants than in vineyards with fewer nearby *Baccharis* plants. Naganuma and Hespenheide (1988) documented plant wound feeding and competitive encounters by three other parasitic hymenopteran families on *Baccharis sarothroides* in Arizona, but extrafloral nectary use by

Ichneumonidae in California is possible. These studies suggest *Baccharis* plays a role in providing alternative hosts and perhaps other resources for Ichneumonidae and could explain the patterns we found.

In the central coast of California, where many farmers are experiencing pressure to remove buffer strips and hedgerows (which often contain *Baccharis*, among other native taxa) at field margins (Beretti and Stuart 2008) and economic incentives continue the loss of farmland to housing development, nearby off-farm vegetation may become the only refugia for natural enemy species and their alternative host species. None of the land use classes associated with this land conversion (e.g. paved roads, commercial/industrial landcover) was negatively associated with Ichneumonidae in our research sites, thus the impact of land conversion appears to be an indirect one via the loss of perennial vegetation. Our research suggests that for the family Ichneumonidae, conserving areas of perennial vegetation, particularly *Baccharis* shrubs, is important for preserving their diversity within central coast agricultural landscapes, but that diversifying crop fields themselves is an important component of conservation planning. Further investigation of Ichneumonidae at the generic, rather than subfamily level, may allow us to identify taxonomic associations with habitat resources that could be manipulated for either local conservation of species richness or for biological control enhancement. Because conservation biological control (Barbosa 1998) is enhanced by increases in enemies of crop pests (e.g. certain campoplegine genera) but may be decreased by hyperparasitism (e.g. ichneumonid subfamily Mesochorinae, which were too rare in our samples to evaluate) or by parasitizing other natural enemies (e.g. diplazontine genera), managing for the “right” biodiversity for control of crop pests may suggest different vegetative planning than managing to conserve Ichneumondiae as a whole.

CHAPTER 2

LANDSCAPES, FARM MANAGEMENT, AND NATURAL BIOLOGICAL CONTROL OF TWO HERBIVORE SPECIES

Abstract

Landscape-scale vegetation may support local persistence of arthropod natural enemies that regulate herbivorous pests through conservation biological control, but the importance of landscape factors is rarely tested concurrently with evaluation of and on-farm management practices for pest control. We examined how parasitism of two sentinel herbivore species (*Trichoplusia ni* and *Brevicoryne brassicae*) varied across a series of on-farm practices and landscape factors, including crop diversity, tillage frequency, pest controls, and cover of different vegetation types surrounding 33 organic vegetable farms at two spatial scales. Factors that affected parasitism of *T. ni* larvae varied temporally and depended on the dominant parasitoid species. In May, parasitism by *Hyposoter exiguae* was positively associated with annual crop and grassland cover, whereas in September, *Microplitis alaskensis* activity was positively associated with grassland cover, pest control intensity, and decreasing tillage. Parasitism of *B. brassicae* was not associated with either the amount or type of natural vegetation in the surrounding landscape nor with farm management practices. This limited evaluation of parasitism-landscape associations does not support a

common approach to conserving both biological diversity and biological control services.

Introduction

Persistence of natural enemies in agricultural systems is important for biological control of pests but management practices often reduce on-farm availability of resources vital to parasitoids. The disturbance regimes associated with annual cropping systems degrade or remove natural enemy habitat (Landis and Menalled 1998), leaving the farms particularly vulnerable to pest outbreaks (Letourneau and Altieri 1999). Parasitic wasp species are particularly susceptible to loss of habitat resources including food (hosts and carbohydrates), microclimate, and shelter (particularly for pupal development) (Beane and Bugg 1998, Riechert 1998, Pfiffner and Luka 2000). Noncrop vegetation within an annual cropping system provides access to floral nectar that can increase the longevity and oviposition success of some parasitoid species (Idris and Grafius 1995, Baggen and Gurr 1998, Lee et al. 2004), as well as alternative or overwintering hosts (Corbett and Rosenheim 1996). Tillage practices can be destructive to populations of species that are relatively immobile during larval and pupal development (Herzog and Funderburk 1986). Without resources to maintain enemy populations on farms, natural enemies are forced into patterns of “cyclic colonization” after each systemic disturbance (Wissinger 1997) or into more continuous “commuting” (Jervis et al. 1993) between fields and nearby floral patches (Lavandero et al. 2005). Because agricultural intensification has reduced on-farm noncrop vegetation (Matson et al. 1997), remnant vegetation near farms and practices that reduce within-crop disturbance should play vital roles in the persistence of local natural enemies.

Noncrop vegetation near farms can be sources of natural enemies. Kruess and Tscharntke found a positive relationship between refuge proximity and parasitism levels of target herbivores (1994) and that natural enemies had a larger minimum refuge size requirement than did herbivores (2000). Thus the amount of noncrop vegetation, typically defined as forest or grassland cover, near to farm fields can affect the persistence of parasitic wasps and the pest control they provide. Evidence supports the theory that landscape-scale noncrop vegetation is associated with pest regulation. In a review of relationships between natural enemies and agricultural landscapes, Bianchi et al. (2006) found that natural enemy populations were higher (74% of cases) and pest pressure lower (45% of cases) on crops growing within more complex landscapes (greater noncrop vegetative cover) than in simpler ones (less noncrop vegetation).

The majority of cases reviewed by Bianchi et al. (2006) measured predation. The few cases that included parasitic wasps (Marino and Landis 1996, Menalled et al. 1999, Thies and Tscharntke 1999, Menalled et al. 2003, Bianchi et al. 2005, Roschewitz et al. 2005, Thies et al. 2005, Thies et al. 2008, Rusch et al. 2011) have yielded ambiguous results: parasitism was higher in a more complex landscape in one site but did not differ between simple and complex in two other sites (Menalled et al. 1999); relationships between parasitism and landscape complexity displayed temporal variability in some cases (Menalled et al. 2003, Thies et al. 2008); but more consistently positive associations were found in other cases (Thies and Tscharntke 1999, Thies et al. 2005, Rusch et al. 2011).

Understanding how parasitic wasps use particular vegetation types may help explain these variable outcomes. Marino et al. (2006) compiled food plant ranges for common North American lepidopteran pest species, their parasitoids, and the food sources of the parasitoids' alternate hosts. Based on alternative host plant use, they predicted that a combination of ruderal, shrubby, and forested vegetation would best conserve the suite of generalist and specialist parasitic wasps (Marino et al. 2006). Bianchi et al. (2005) found that pasture was strongly associated with parasitism of one pest species, but parasitism of a different pest species was associated with nearby forest (Bianchi et al. 2008). Bianchi et al. (2006) found that predation and parasitism of agricultural pests were more often associated with herbaceous-plant dominated landscapes than with wooded ones though both cover categories were positively associated with natural enemy activity. While maximizing availability of a particular vegetation type may increase population size of a particular enemy species, the presence of multiple vegetation types (greater vegetative richness) may support a more diverse and temporally stable natural enemy community (Chaplin-Kramer et al. 2011), which often leads to greater pest control (Letourneau et al. 2009). Menalled et al. (2003) found that the relative dominance of particular enemy species varied among years and locations, and appeared to drive variation in landscape-parasitism relationships. Greater vegetative diversity, not just greater vegetative area, at a landscape scale may reduce temporal variability.

A mosaic landscape perspective allows investigation of the relative contributions of patches of various vegetation types to the control of agricultural pests. However, agricultural fields often are situated amidst patches converted to nonagricultural purposes; high speed roadways cause significant mortality for flying insect taxa like Odonata (Soluk et al. 2011) and Lepidoptera (Rao and Girish 2007). Jonsson et al. (2012) found that parasitism was negatively associated with the amount of landscape scale annual crop cover but had no relationship to noncrop vegetation diversity. In addition, rural (i.e. isolated homesteads), residential, commercial, and industrial landuses represent decreasing and homogenizing vegetative and increasing impervious cover, thus potentially diminishing resources available to natural enemies. A mosaic landscape perspective allows for investigation of particular landuse as well as vegetation types.

Management intensity varies among farms, and landscape-scale resources may be more important for natural enemy populations in more intensively managed farms. In particular, lower tillage (Wissinger 1997) and pesticide application frequency (Ohnesorg et al. 2009, Geiger et al. 2010) and greater crop diversity (Letourneau et al. 2011) may compensate for scarce resources for natural enemies in simple landscapes but have less effect in more complex ones, as was found for pollinators (Batary et al. 2011). A few studies have examined the combined effects of landscape and farm management on biological control. Roschewitz et al. (2005)

found that parasitism of cereal aphid was positively associated with landscape complexity but not associated with farm management (defined as organic versus conventional), Woltz et al. (2012) found that coccinelid beetle abundance was higher in fields surrounded by more noncrop vegetation but predator abundance was unrelated to landscape diversity (Simpson's index applied to vegetation and landuse classes) or farm management (presence of floral field margins), and that predation rates were too uniformly high in all sites to compare. Holzschuh et al. (2010) determined that predatory wasps were more abundant in less intensively managed fields but unrelated to noncrop vegetation at the landscape scale, and that parasitoid patterns were mediated by their hosts. Geiger et al. (2010) found that predation of sentinel aphids declined with increasing pesticide use and increased with landscape complexity, and Jonsson et al. (2012) found that parasitism was unrelated to landscape diversity but negatively associated with annual crop cover—a result they attributed to insecticide application rather than to resource disruption. There is a need for more studies that integrate the contributions of both landscape-scale factors and farm management on pest control, particularly with regard to parasitism.

In this study, we investigated the effects of both landscape context and farm management practices upon parasitism of two sentinel crop pests within 33 commercial annual crop fields in the central coast region of California, a geographic area containing diverse natural vegetation. Central coast agricultural landscapes include large-scale intensive crop production, small farms embedded in mixed oak-conifer forests, and complex vegetation-landuse mosaics. We hypothesize that parasitism of crop pests would be greater on farms situated in landscapes containing more noncrop vegetation (hereafter referred to as "vegetation"). Whereas greater noncrop vegetation cover in general should support greater pest control, we also hypothesize that parasitism will be highest on farms situated in mosaics of greater vegetative diversity, benefit more from some types of vegetative cover than others, suffer from proximity of deleterious landuses (such as paved roads), and that intensive farm management practices (e.g., lower crop diversity, more tillage, greater pesticide use) have a greater impact on parasitism where landscape mosaics provide fewer resources to local natural enemies. To test these hypotheses, we measured wasp parasitism of two sentinel pest species, quantified management practices most likely to affect insect populations, and characterized the landscape mosaics around organic farms that represent the range of organic vegetable production in the central coast region.

Materials and Methods

Study region and research sites

The central coast region of California contains a mosaic of natural vegetation, such as wetlands, chaparral, oak woodlands, coniferous forest, and coastal prairies, as well as farming operations and urban development. Its mild Mediterranean climate supports vegetable production year round. Most of the approximately 450 mm average annual precipitation (NCDC 2009) occurs between October and April, and crops are irrigated during the dry May through September months. Annual cropping systems dominate agriculture in the three counties included in this study (Santa Cruz, Monterey, and San Benito), producing 16% of the national and 28% of the Californian market value for vegetables, melons, potatoes, and sweet potatoes with a disproportionately high acreage in organic production (~10% of California organic acres harvested in the tri-county area, within less than 4% of total California acres) in comparison to the rest of the United States; California contains 62% of national organic vegetable production acres (CCOF 2008, USDA 2009). Of approximately 50 certified organic vegetable growers in Santa Cruz, Monterey, and San Benito counties, 25 agreed to host research on the 33 certified organic farm fields (hereafter called sites), that were separated by at least 1 km, and within a one-hour driving distance from the University of California, Santa Cruz. The northern most site (37°06'33.83"N, 122°16'20.06"W) was 60 kilometers north of the southern-most site (36°32'21.30"N, 121°51'45.24"W) and 80 kilometers west of the eastern-most site (36°51'74"N, 121°18'31.42"W) (Figure 1.1). This geographic distribution of sites encompasses coastal areas and inland valleys, which vary in average temperatures, and encompasses the range from simple to complex mosaic landscapes.

Landscape and farm management characterization

In a geographic information system (GIS), we designated 0.5 km (small) and 1.5 km (large) radius circular landscape areas (0.785 km^2 and 7.07 km^2, respectively) around the center point of each site (Fig 1.2) to measure small and large landscape-scale features; these distances were based on prior multi-scale studies of parasitic wasp movement in agricultural landscapes (Letourneau and Goldstein 2001, van Nouhuys and Hanski 2002, Thies et al. 2003) and a recognized need to consider variable scales among species (Steffan-Dewenter 2002). We manually digitized and attributed one of nine landuse (e.g., annual or perennial cropland, paved or gravel roads, industrial and residential areas) or forty-one vegetation classes (e.g., conifer, *Quercus*, or *Eucalyptus* forest, *Salix* or marsh riparian vegetation, *Baccharis* and *Salvia* shrubland, mixed forbs or grassland) to polygons. Vegetation mixes were denoted by dominant taxa in order of their prominence, such as oak-conifer, considering all taxa with greater than 10 percent coverage within the polygon; this yielded several 2- and 3-taxa vegetation classes. Ground-truthing for these categorizations of vegetation, which comprised field-based checks of 300 randomly selected points within the 33 digitized landscapes, showed a >89% accuracy rate. Subtle distinctions in hue and pattern characteristics, such as occur between *Quercus* and *Salix* designations, were the sources of identified attribution error. More detailed methods, the list of 50 distinct land-cover categories, and a description of our quality assessment process are located in Appendix 1. We used these data to generate percent land cover estimates for all cover types present in the 33 small (0.5km radius) and large (1.5km radius) landscapes (A1).

To reduce this large number of dependent variables, some of which covaried, we conducted Principle Component Analyses (PCA). Vegetation and landuse types present in very few landscapes (e.g., "*Acacia*" was present in only two landscapes) or represented less than one percent of cover in any landscape (e.g. "*Baccharis*-grass" and “grass-forbs”), were grouped into larger categories based on dominant vegetation (e.g. “*Baccharis*” comprising *Baccharis* alone, *Baccharis*-grass, and *Baccharis*-hemlock classes) and/or broader relationships (grasslands, perennial vegetation, and noncrop vegetation), allowing us to include data from variables that otherwise would have been excluded to meet the assumptions of PCA. Additionally, we created a vegetation richness variable—the number of noncrop vegetation classes present in each landscape. Based on these adjustments, we included 17 classes in the large scale PCA and, separately, 15 classes for the small scale PCA. Components were selected based on Eigenvalues greater than one.

We measured three farm management factors that are known to influence resource availability for natural enemies: crop diversity, tillage, and pesticide application. Crop diversity values one through four were assigned in ascending order for monoculture, *Brassica* and *Lactuca* crops, two to three additional plant families, and more than four plant families, based on the average number of crops grown per field in 2004-2006. Tillage disturbance was counted as the number of crop transitions per year, when the entire vegetative structure of a field was disked into the soil before replanting. Pesticide use severity was calculated as a sum of all insecticide (USDA National Organic Program allowed substances) applications or vacuuming multiplied by a weight based on the breadth and duration of action for each substance (weights: 0.25 = vacuum; 1 = soaps, oils, Bt; 2 = pyrethrum, spinosad). Weights were assigned based on whether they affect Hymenoptera directly (e.g. pyrethrum), only indirectly through host population reduction (e.g. Bt), or by the extreme frequency of their use (vacuuming).

Sentinel pest exposure

Two herbivorous species were used as sentinels to detect levels of parasitism present at each site. *Trichoplusia ni* (Noctuidae) hosts at least three genera of parasitoids (Flint and Dreistadt 1998) and is a common pest, feeding on numerous host plant species, including some of the most common crops in the study region (*Brassica, Lactuca*, and tomato crops) (Shelton et al. 1982). *Brevicoryne brassicae* (Aphidae) is a ubiquitous and challenging pest of *Brassica* crops in the Central Coast region due to rapid population growth (Flint 1990), and can cause damage that renders crops unmarketable; their control is important to local farmers. Parasitism by the braconid wasp *Diaretella rapae* is an important component of that control.

Sentinel experiments were conducted in May, July, and September 2005-2007 (*T. ni*) and in May and August 2006 (*B. brassicae*). We report methods and results for *T. ni* in May and September 2007 only because methodological differences in 2005 resulted in parasitism by Tachinidae (Diptera) which is reported elsewhere (Letourneau et al. *in review*), and because of ubiquitous low parasitism levels in all trials in 2006 and in July 2007. For methodological variations on this experiment used in 2005 and 2006, see Appendix 3. In 2007, five of the 33 sites were not in production.

T. ni sentinels were used to detect parasitism in May, July, and September. Because of the variability in crop diversity and quality among sites, *T. ni* eggs were placed on greenhouse grown, potted, collard plants inside individual fine mesh exclosures to prevent pre-experiment parasitism of emerging larvae. After two days, ten plants in one gallon pots containing first instar larvae were placed at 28 sites and left for seven exposure days. Twelve second to fourth instar *T. ni* larvae were haphazardly collected from each plant at the end of the exposure period, for a total of 120 larvae per site, and reared on artificial diet in a growth chamber at 27 degrees Celsius with a 16:8 day-night cycle. Percent parasitism per plant was determined as the number of parasitized larvae (parasitoid emerged or immature parasitoid detected in dead larvae) divided by the total number of larvae collected per plant. Site parasitism level was the mean of all ten plant means. Missing values were generated rarely (e.g., large-scale mortality due to Bt-pesticide application by farm staff or unusually high level of attack by spiders which resulted in collection of fewer than 120 larvae).

B. brassicae sentinels were used to detect parasitism in May and August 2006. We established unparasitized colonies of *B. brassicae* on potted collard seedlings in four-inch pots in a greenhouse on a 12:12 day-night cycle. Five experimental colonies were placed within crop fields in May (26 sites) and August (33 sites) 2006. The sentinels were exposed for 48 hours, and then returned to parasitoid-exclosure cages to monitor for mummy development. Additional colonies on identical potted collard plants were retained in the parasitoid-exclosure cages to measure a baseline level of parasitoid infection within the cages. We monitored the colonies daily for mummies over a period of ten (May) and 13 (August) days—until no novel mummies were observed for two days. Mummies were collected in gelatin capsules and parasitoids were allowed to emerge under greenhouse conditions. Site parasitism level was calculated as the percentage of colonies displaying any parasitism—that is, presence/absence scores for each of the five colonies.

Data analysis

To test whether there was a relationship between noncrop vegetation and parasitism, we conducted a regression of the percent of each sentinel species parasitized with the amount of noncrop vegetation surrounding the sentinels at both the larger and smaller landscape scales. To test whether particular landscape or farm management factors were associated (positively or negatively) with parasitism, we conducted multiple regressions in PC-SAS version 9.2 (SAS 2003), using the first five principle landscape components and the three management factors (a suite of 8 variables), and repeated these analyses for both 1.5km and 0.5km landscape scales and for both sentinel species. We used AIC values (Beal 2005) to select models that best describe the distribution of parasitism data. Models with AIC values at least 1-integer lower than alternative models were considered to best explain the distribution of parasitism; models including fewer variables were selected for tests yielding equivalent alternative models (<1-integer difference in AIC scores). In the case where highly complex models yielded the lowest AIC scores, selection was based only on models containing four or fewer variables, Landscape variables that were strongly loaded (>0.35) on significant components were considered to be explanatory.

Results

Farm management and landscape complexity

Noncrop vegetation cover across the 33 landscapes included in this study ranged from 2% to 97% (1.5km scale) and from 1% to 89% (0.5km scale). At the 1.5km landscape scale, noncrop vegetation was composed primarily of coniferous forest (mean = 19%), grassland (16%) and California live oak forest (9%) while at the 0.5km landscape scale, noncrop vegetation area was primarily grassland (15%), coniferous forest (14%), and residential areas (11%). Individual landscapes ranged from intensively managed agricultural landscapes (Fig. 1.2a), to remote farms surrounded by a few vegetation classes, to complex mosaics including multiple vegetation and landuse classes (Fig. 1.2b). Vegetation and landuse classes that represented at least one percent cover (Table 1.1) were included in the PCAs. For a complete list of vegetation and land use classes by area for each site, see Appendix 1. PCAs of the vegetation and landuse variables yielded five explanatory components at both the 1.5km (LC1-5, explaining 75 percent of the variance) and 0.5km scales (SC1-5, 74 percent of variance) (Table 1.2). Farm size among the 33 sites ranged from 0.01 to 1 km^2, crop diversity from one to four (monoculture through polyculture including at least four plant families, mean = 2.6 ± 1.1SD), tillage frequency from one to four major events per year (mean = 2.6 ± 0.9SD), and pesticide severity from zero to 15 (ranging from no actions to scheduled vacuuming and insecticide applications, (mean = 1.4 ± 2.9SD). Pearson's correlation tests among pairs of landscape components and farm management factors yielded only one significant relationship: a negative association between crop diversity and pesticide use severity ($R^2 = 0.1799$, p = 0.0139).

Parasitism of sentinel pests

Parasitism of *T. ni* sentinels was low in July (no parasitism measured at 19 of 28 sites) and so was excluded from analysis, but higher in May (parasitism at 13 of 28 sites, up to 78 percent) and September (19 sites, up to 24 percent) (Figure 2.1). Parasitism rates of *T. ni* larvae in May and September were analyzed separately to detect whether the relationship between landscape and parasitism varies with season.

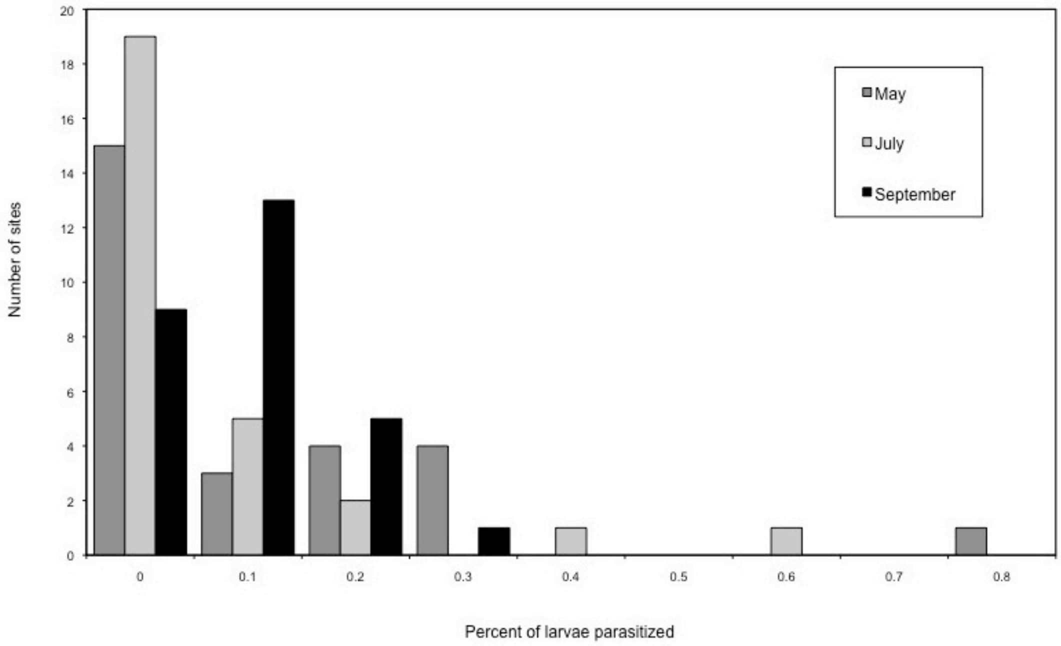


Figure 2.1. Distribution of parasitism levels on sentinel *T. ni* larvae in spring, summer and fall of 2007.

Parasitism of *T. ni* sentinels was not associated with the amount of noncrop vegetation in agricultural landscapes at the 1.5km landscape scale (R^2 = 0.072, p = 0.177) and negatively associated at the 0.5km landscape scale (R^2 = 0.152, p = 0.044, Fig. 2.2). Regression analysis indicated that different models best explained parasitism in May and September, although landscape component four (LC4) was common to both models. Results were similar for both landscape scales, so we report here only results for the 1.5km scale except where differences exist. In May, parasitism was positively associated with LC1 (high cover of annual cropland, and low covers of *Baccharis*, perennial vegetation, and noncrop vegetation) and LC4 (high perennial crop and grassland cover, and low freshwater cover) (F = 8.28, p =

0.0083, $R^2 = 0.2916$) (Fig. 2.3). This association with LC1 is consistent with the negative relationship between parasitism and 0.5km scale noncrop vegetation—annual cropland comprised much of the remaining landcover in many landscapes. In September, the three-variable model best associated with *T. ni* parasitism included positive relationships with pesticide use severity and LC4 but a negative association with tillage intensity (F=10.75, p = 0.0001, $R^2 = 0.6218$) (Fig. 2.3).

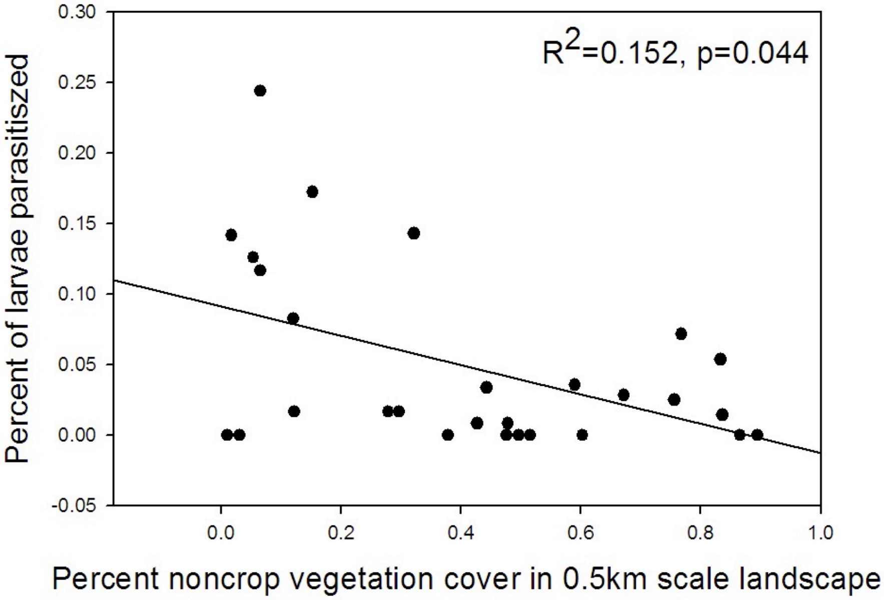
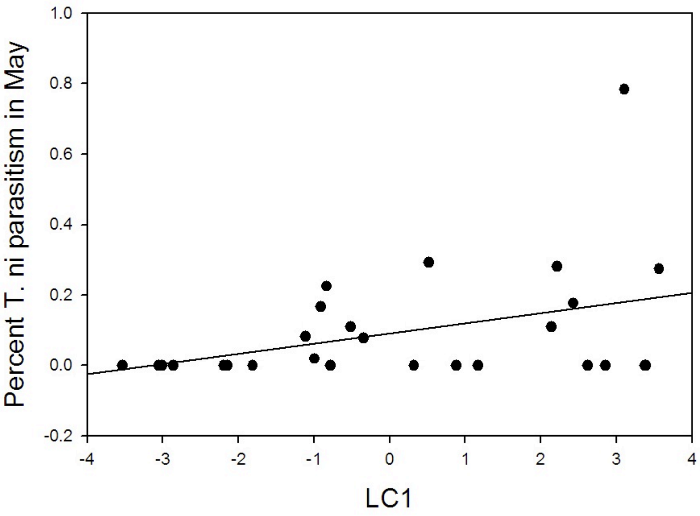
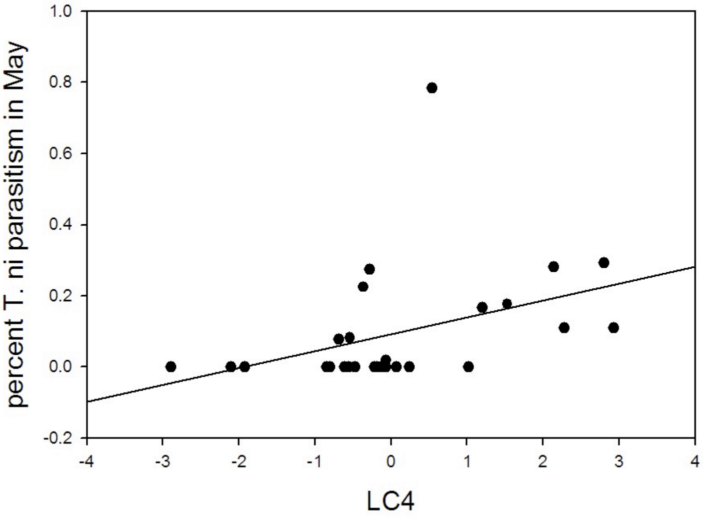
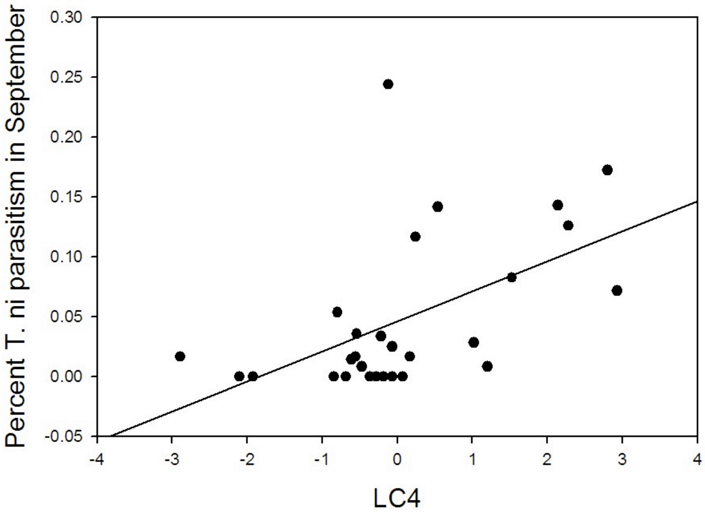


Figure 2.2. Negative relationship between *T. ni* parasitism and vegetative cover at the 0.5km landscape scale.


Percent T. ni parasitism in May
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-4
-3
-2
-1
0
1
2
3
4
LC1


percent T. ni parasitism in May
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-4
-3
-2
-1
0
1
2
3
4
LC4


Percent T. ni parasitism in September
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-4
-3
-2
-1
0
1
2
3
4
LC4

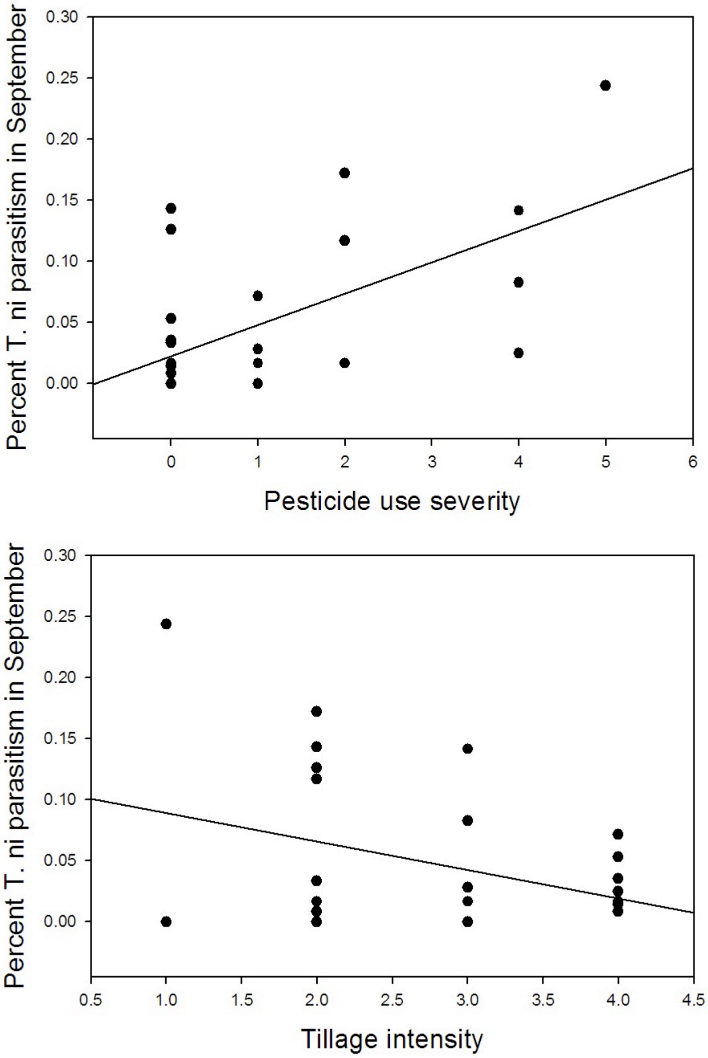


Figure 2.3. Regressions of *T. ni* parasitism in May with 1.5km landscape components one (LC1) and four (LC4) ($R^2 = 0.2916$, $p = 0.0083$) and in September with 1.5km landscape component four (LC4), pesticide use severity, and tillage intensity ($R^2 = 0.6218$, $p = 0.0001$).

Five wasp species (three Ichneumonidae and two Braconidae) and a suite of flies (Diptera: Tachinidae) were responsible for the parasitism of sentinel *T. ni* larvae. *Hyposoter exiguae* (Ichneumonidae) parasitized a majority of the sentinel larvae (58%), particularly in May (85 percent). *Microplitis alaskensis* (Braconidae) was the second most common overall (23 percent), and was more frequent (58 percent) than *H. exiguae* in September. The remaining parasitism was due to Tachinidae (Diptera) (10 percent), *Cotesia* sp. (Braconidae) (three percent), Ichneumoninae sp. (two percent), and *Therion californicum* (Ichneumonidae) (less than one percent). Parasitism by *H. exiguae* and *M. alaskensis* in May and September, respectively, drove the overall parasitism associations we found. In May, parasitism by *H. exiguae* was positively associated with LC1 and LC4 (F= 4.83, p = 0.0173, R^2 = 0.2866). In September, parasitism by *M. alaskensis* was positively associated with pesticide use intensity and LC4, and negatively associated with tillage intensity (F= 6.50, p = 0.0024, R^2 = 0.4924).

Parasitism rates of *B. brassicae* ranged from 0 to 5 colonies per site (mean = 2.25 ± 1.47SD) (Fig. 2.4), with no association with noncrop vegetation cover in May (R^2 = 0.004, p = 0.75) or in August (R^2 = 0.044, p = 0.24). In May, *B. brassicae* colony parasitism showed a marginal positive association tillage disturbance (R^2 = 0.143, p = 0.0571, Fig. 2.5a), and in August, aphid parasitism was positively associated with crop diversity (R^2 = 0.136, p = 0.035) (Fig. 2.5b) but with no other factors.

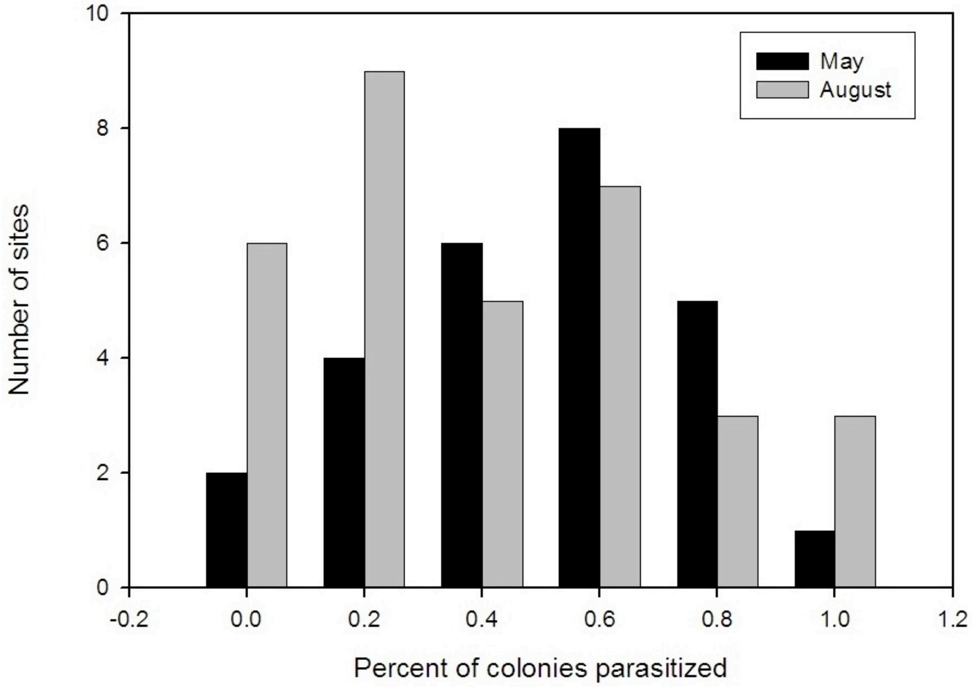


Figure 2.4. Distribution *B. brassicae* colonies parasitized in May and August 2006.

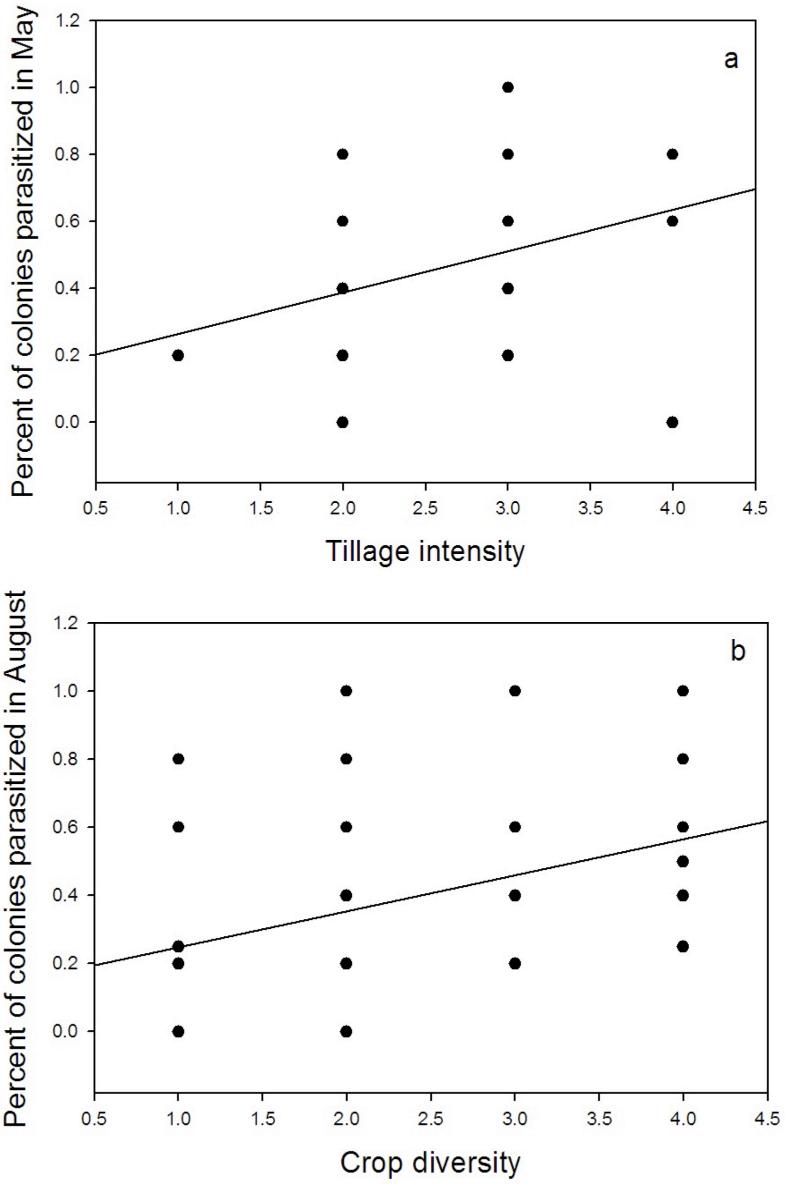


Figure 2.5. Relationships between parasitism of *B. brassicae* colonies (a) in May with tillage intensity ($R^2 = 0.143$, $p = 0.0571$) and (b) in August with crop diversity ($R^2 = 0.136$, $p = 0.035$).

Discussion

Contrary to our hypothesis, parasitism of sentinel pests was not positively associated with the amount of landscape-scale noncrop vegetation, for *T. ni* or *B. brassicae*. Instead, however, parasitism of *T. ni* by two dominant parasitoids varied with landscape and farm management factors. The parasitoid *H. exiguae* was negatively associated with perennial vegetation cover in general and *Bachharis* cover in particular, contradictory to prior findings (Kido et al. 1981, Bianchi et al. 2008). *H. exiguae* parasitism was also positively associated with annual crop cover. Of the few prior studies investigating landscape contributions to parasitism, none has previously reported a positive association with annual crop cover, although Jonsson et al. (2012) found a negative relationship. *Hyposoter* species attack a number of lepidopterous agricultural pests (Flint and Dreistadt 1998) and may be adapted to the high-frequency disturbance regime of annual cropping systems (Ehler and Miller 1978), although such disturbance is considered an overwhelming challenge to successful biological control (Wissinger 1997). Rather than commuting to floral resources, *H. exiguae* movement at the landscape scale may be driven by locating hosts within agricultural patches. The availability of annual crop patches throughout a landscape may provide refuges in space from tillage events on individual farms. In the case of *M. alaskensis*, the negative association with tillage frequency indicates the deleterious effect of one measure of annual cropping intensity. Pesticide use severity, on the other hand, was positively associated with parasitism. This result, however, seems driven by a relatively high parasitism rate at one of the few farms employing vacuum pest removal rather than insecticide spraying. Although vacuum removal is broad-spectrum in action compared to the taxon-specific action of Bt applications, for example, the brevity of its action may allow for quicker community-level recovery.

One landscape factor, LC4, was positively associated with *T. ni* parasitism in both May and September, thus indicating a relationship with both dominant parasitoids. LC4, with strong positive loadings from grassland cover and perennial cropland and negative loading from freshwater, represents the importance of landscape-scale resources beyond annual crop cover. California coastal grasslands contain numerous forb species; some may provide floral resources while others likely provide hosts—wild relatives of *Brassica* crops are common in the region. Negative associations with perennial cropland and freshwater are surprising. One might expect the opposite—that the relative humidity near freshwater resources might compensate for a negative impact of California climate on parasitoids in grass or shrublands, which flower in spring and then desiccate through summer. Instead, relatively higher humidity within these irrigated crop fields may balance out climatic and riparian cover effects. LC2, which carries strong loadings of the hypothetically deleterious landscape features paved road and commercial/industrial cover, had no relationship with *T. ni* parasitism. The relationship between parasitism of *T. ni* and the availability of landscape-scale resources to parasitoids is not a simple, positive association, yet the differences we observed between May and September support the hypothesis that greater landscape complexity can help reduce temporal variability in pest control.

For *B. brassicae*, the variation in parasitism showed no relationship to landscape-scale factors and little influence of farm management. In fact, the ubiquity of cabbage aphids at relatively low densities across vegetable farms in this region (personal observation) may be the most important factor for supporting resident parasitoid populations. Rauwald and Ives (2001) suggest that the life history of the pea aphid parasitoid, *Aphidius ervi*, endoparasitic in still-living hosts, is what facilitates its rapid recolonization and successful pest suppression in high intensity alfalfa production. Parasitism of *B. brassicae* at our sites, and perhaps of other aphid species may be successful for the same reason.

These results expand upon existing understanding of the relationship between landscape factors and pest control by documenting a rare negative association between landscape-scale noncrop vegetation and parasitism as well as the positive relationship with annual crop cover. These findings could place pest control at odds with biodiversity conservation goals in agricultural landscapes; Ichneumonidae species richness displays the opposite pattern at our sites (Chapter 1). However, Ichneumonidae is a highly diverse family utilizing an equally diverse range of host species. The variety of responses we found to both landscape and farm management factors for two sentinel species on one crop species suggests that many more patterns may be discovered within the entire mixed-vegetable production system, or by other parasitoids more dominant in other years. For vegetable cropping in the California central coast region, in which numerous herbivore-parasitoid relationships exist, more data within cropping systems is necessary for understanding the community ecology of and potentially managing agricultural landscapes to support this ecological service.

CHAPTER 3

LIMITATIONS OF INDICATOR TAXA: ICHNEUMONIDAE AS A CASE STUDY

Abstract

Biological indicator taxa may be useful tools when assessment when the direct assessment of biological diversity or ecological services is impractical. However, the limitations of using indicator taxa are often unknown, especially when a single indicator is used, and there have been few quantitative assessments of the how well particular taxa work as indicators. I review examples of effectiveness of indicator taxa used to infer biological services for agriculture, and illustrate some limitations of their use with original data on parasitic wasp abundance and parasitism of a sentinel pest. For example, neither abundance nor species richness of parasitic wasps (Ichneumonidae and the subfamily Campopleginae) within organic vegetable fields was correlated with parasitism of *Trichoplusia ni*, another measure of biological control. For even relatively simple communities, such as those in agroecosystems, multiple indicator taxa may be needed for an appropriate assessment of biodiversity and ecological services.

Introduction

Current conservation planning involves efforts to conserve or restore biological diversity that provide ecological services (Balvanera et al. 2001, Benayas et al. 2009). Whether such conservation efforts actually result in greater pollination and biological control services is of great interest farmers who manage organic or low-input production systems (personal communications with 34 California central coast growers and farmers). When asked, “Does increasing on-farm diversity of predators and parasitoids through habitat management benefit their pest control interests?” their unanimous answer was “yes” —a position supported by local farming nongovernmental organizations (WFA 2005, CAFF 2006) that promote conservation and restoration of on-farm natural enemy habitat. However, there is a need for reliable metrics of “beneficial” biodiversity that farm owners, ranch managers, and pest control advisors could use to evaluate on-farm pest suppression potential. Some beneficial insects are relatively easy to identify and count (e.g., *Hippodamia convergens*) where as others (e.g., most parasitic wasps and flies) are much more difficult. Identifying indicators for these more challenging groups will allow broader testing of whether their diversity provides a pest control benefit to farmers. Here, I examine issues with developing and using indicators, review current knowledge regarding the relationship between natural enemy diversity and pest suppression, and provide a partial test of Ichneumonidae as an indicator of biological control service.

Selecting "indicator" taxa

Measuring a subset of the diversity of an area to as a proxy for total biological diversity has become a popular practical approach for conservation planning (Kremen et al. 1993, Hyatt 2001, Mace and Baillie 2007). The monetary and time costs and expertise requirements limit the practicality of complete biological inventories. Similarly, limited resources have focused conservation efforts on protecting areas of high biodiversity, often relying on subset-sampling to evaluate overall biodiversity of an area. This approach of focusing on a subset of biota to represent the whole has received many names: indicator (Maleque et al. 2006), surrogate (Lovell et al. 2007, Rodrigues and Brooks 2007), proxy (Sarkar and Margules 2002), and target (Kremen 1994). While some researchers define the term "indicator" to be an environmental measure while "surrogate" is a subset of biota to represent the whole (Rodrigues and Brooks 2007), most researchers do not draw this distinction. Some researchers distinguish between "true" and "estimator" indicators. In this dichotomy, true indicators should represent the actual target biota whereas estimator indicators would instead refer to a true indicator—an additional level of abstraction in representing the target biota (Sarkar and Margules 2002). In this chapter, I will use the term "indicator" to refer to the entire approach of using a particular group of organisms as a proxy for the biotic community as a whole, because the focal taxon is being used to reflect the condition of a larger suite of species and to make assumptions about functional aspects in the ecosystem.

Potential indicators should be chosen based on qualities that make them likely candidates for truly representing the target biota (e.g., a strong correlation with the target biota across habitat changes), for ease of measurement (e.g., easily identified), and for low response variability (Kremen 1994, Tscharntke et al. 1998, Dale and Beyeler 2001, Lovell et al. 2007, Hirst 2008). In a recent review of 27 studies, providing 575 tests of the relative value of potential indicator taxa and environmental factors, Rodrigues and Brooks (2007) found evidence that indicator taxa are better than environmental indicators as proxies for target biota. Indicator taxa that overlap (share some species in common or are a subset) of target taxa are better than indicators that do not (Rodrigues and Brooks 2007).

Arthropods can be useful indicator taxa for biodiversity more generally because of their high species richness, broad range of ecological functions (Maleque et al. 2006), and responsiveness to changes in habitat quality (Tscharntke et al. 1998). Most arthropod-based indicator studies have focused on a subset of arthropod diversity rather than on the diversity of this enormous group as a whole. In these studies, particular insect taxa are proposed as indicators under specific geographic or functional conditions, although degree of testing among proposed taxa to evaluate usefulness in answering specific ecological questions varies among studies. For example, Kremen (1994) tested the indicator values of a genus and a subgenus of butterflies endemic to Madagascar as proxies for the diversity of all Madagascar butterflies. Strength of correspondence to the entire butterfly fauna was higher for the subgenus, and a large-scale estimate of butterfly diversity could be extrapolated from diversity surveys of this one subtaxon (Kremen 1994). In this example, Kremen's (1994) argument for a single-taxon approach to arthropod indicators—that the spatial distribution of multiple endemic clades should be positively correlated—was supported. However, Baldi (2003) found that one taxon (i.e., Order: Coleoptera) was not a good indicator for the species richness of another order of insects (Diptera). A comparison of indicator value among several subsets of Arthropoda found a lack of congruence across the arthropod taxa sampled, and so a single indicator taxon should not be used to represent all arthropod diversity; a multi-taxa approach could provide more robust congruence to the target group (Lovell et al. 2007). It seems that different approaches may be used, provided the proposed indicators are tested.

Indicator taxa have also been used to represent a variety of environmental conditions. Particular target species have been used as indicators of environmental health, such as air (Divan et al. 2009) and water quality (Siriwong et al. 2009). A community-level approach has been more common than single species abundance or presence-absence monitoring for evaluating conservation-oriented environmental health concerns, such as the effect of silvicultural techniques on forest health (Maleque et al. 2006, Deans et al. 2007, da Silva et al. 2008) or management tactics on agroecosystem health (Tscharntke et al. 1998, Matlock and de la Cruz 2003). Subgroups of arthropod diversity have been a recent focus as forest health indicators. However, taxon selection is often based on a range of expected effectiveness and logistical feasibility criteria rather following actual testing of those taxa as reliable indicators of environmental endpoints. Samples of flies in the family Syrphidae

(Order: Diptera) were used to evaluate impacts of a range of forest harvesting techniques upon greater biodiversity (because they are sensitive to subtle habitat changes) and ecosystem health (because they may perform multiple ecological roles) (Deans et al. 2007). Deans et al. (2007) identified timber harvest practices associated with the highest Syrphidae diversity, but they simply assumed they would also be good indicators of their expressed targets: biodiversity and forest ecological health. Diversity of several hymenopteran families were associated with a new, less destructive silvicultural practice, compared to conventional, but Maleque et al. (2006) also did not evaluate whether hymenopteran family diversity was a robust indicator for either biodiversity or ecological health. Both papers present logically reasonable selection criteria for their selection of indicator taxa, but neither empirically demonstrated their value. Skipping this step can be problematic. Da Silva et al. (2008) selected Carabidae (Order: Coleoptera) species richness as an indicator taxon for forest health due to its diversity, ubiquity, sensitivity to habitat changes, and prior use by other researchers. The highest carabid species richness they detected, however, was in the most intensively managed (and assumed to be most ecologically compromised) of the systems they compared (da Silva et al. 2008), thereby casting doubt on the utility of theoretical logic alone to select indicator taxa; among species known to be more sensitive to disturbance, fewer were located in the intensively managed systems.

In an agricultural health context, appropriate indicator selection has been better emphasized. Matlock and de la Cruz (2003) did not directly test ant species richness as an indicator of greater biodiversity or agroecosystem health. However, they cited prior research by others that demonstrated a correlation between ant biodiversity and greater faunal diversity and cited direct tests of ant species richness as an indicator taxon for ecosystem restoration. For Matlock and de la Cruz (2003), however, their target was agroecosystem health, for which ants were determined to be an inappropriate indicator due to their relative insensitivity to the pesticides used in the conventional banana system they studied. They proposed that parasitic Hymenoptera, whose diversity correlated with that of the ants and whose sensitivity to pesticides appeared much stronger, should be a better indicator group (Matlock and de la Cruz 2003). Tscharntke et al. (1998) evaluated the appropriateness of species richness of a suite of bee and predatory wasp families as an indicator for ecological functions by measuring differences not only in species richness of their focal taxa among habitat types, but also by measuring parasitism by their natural enemies—in this case, higher parasitism levels were intended to more broadly indicate community health, even if it resulted in some level of suppression of the pollination and biological control services supplied by the host bees and wasps. They found that bee species richness was more highly correlated with the habitat parameters they measured than was wasp species richness and that parasitism was related to habitat; they did not directly test for a relationship between the richness of the wasps and their rates of parasitism (Tscharntke et al. 1998). While testing potential indicators is challenging, an indicator taxon is a level of abstraction beyond measuring the attribute itself, and thus testing is the only means by which we can evaluate its probability of indicating correctly.

The natural enemy diversity and herbivore suppression

Species richness of particular taxa has often been tested as indicators of environmental quality or function. Such diversity-function questions date back to MacArthur's (1955) suggestion that more diverse food webs should also be more stable. Subsequent work suggested mechanisms, such as insurance against loss of functional groups, by which larger numbers of species could provide systemic stability (McNaughton 1977, Naeem and Li 1997, Naeem 1998). Population sizes of insect species may demonstrate substantial inter-annual fluctuation (Davidson and Andrewartha 1948), and so functions such as herbivore regulation may be most stable in species-rich areas, where temporal fluctuations of a particular species will be damped by functionally equivalent species in the community. Gratton and Welter (1999) found different species were responsible for the majority of parasitism of a leafmining fly among three consecutive years, with two years being dominated by specialist parasitoids and one year dominated by a single generalist species. However, the diversity-stability relationship is not always consistent, particularly in cases measuring higher trophic levels (Hooper et al. 2005).

While the relationship between biological diversity and temporal stability of ecological functions may not be true for all communities, numerous tests of natural enemy species richness as an indicator for herbivore suppression reflect interest in applying this hypothesis to natural biological control theory, which contrasts with the theory and many examples from classical biological control, in which establishment of one particularly enemy species often leads to the best pest suppression (DeBach and Rosen 1991). Earlier research engaged these contrasting perspectives indirectly in the context of community and functional responses to vegetation diversity (Letourneau 1987). By extending this line of inquiry to include higher trophic levels, the suite of direct and indirect effects expands dramatically and makes the influence of diversity at one level more challenging to isolate. As a result, there have been many recent direct laboratory and field tests of the relationship between natural enemy diversity and herbivore suppression, particularly in the context of biological control research. Recent reviews of that literature (Straub et al. 2008) and of diversity-suppression both in agricultural and natural systems (Letourneau et al. 2009) summarize the evidence and theoretical mechanisms behind the three potential types of relationship: positive, negative, or neutral.

Evidence for a positive relationship:

There are numerous examples of a positive correlation between natural enemy diversity and pest suppression, measured as predation (Losey and Denno 1998, Snyder and Wise 2001, Wilby et al. 2005, Snyder et al. 2006), parasitism (Kruess and Tscharntke 1994), a combination of the two (Cardinale et al. 2003, Schmidt et al. 2003, Snyder and Ives 2003, Straub and Snyder 2008), relative pest population size (Cardinale et al. 2003, Snyder et al. 2006), or crop yields (Snyder and Wise 2001, Cardinale et al. 2003, Snyder et al. 2006, Straub and Snyder 2008). Communities in which multiple natural enemy species collectively consume greater numbers of their resource (prey or host insect) suggest resource complementarity through resource partitioning or facilitation. Straub and Snyder (2008) showed evidence of resource partitioning where different natural enemy species foraged in different locations on the host plants, thereby accessing different prey individuals. Losey and Denno (1998) found that when aphids dropped off their host plants to avoid one predator they then became available to a soil-foraging predator. Cardinale et al. (2003) found that the positive relationship between natural enemy species richness and parasitism of a focal species was driven by the presence of an alternative prey species.

Evidence for a negative relationship:

Herbivore suppression can also diminish as natural enemy diversity increases (Rosenheim et al. 1993, Snyder and Wise 2001, Finke and Denno 2005). Intraguild predation (IGP) and parasitism disruption (such as by hyperparasitoids) are two mechanisms that lead to herbivore release in communities with high natural enemy diversity, though IGP alone has been the focus of the most research (e.g. the same list of papers above). However, IGP's impacts on herbivore suppression or release are not always consistent. Snyder and Wise (2001) found that IGP occurred only in a late summer crop but not during spring. Snyder and Ives (2003) found IGP within a predator-parasitoid enemy mix, but no evidence that it reduced the density-dependant attack of the parasitoid on its host aphid nor the supplementary control exerted by the predator. The predator-parasitoid mix still produced an additive level of suppression compared to the two enemies independently. This "coincidental IGP" occurs because the impact on herbivore suppression is less when a parasitoid and its host are simultaneously depredated, compared to "omnivorous IGP" in which one predator species depredates a second directly (Straub and Snyder 2008). Other experiments, such as Schmidt et al. (2003) in which herbivore suppression is compared among a suite of natural enemy functional groups can mask the evidence of coincidental IGP, if its negative effect is relatively small compared to the positive effect of resource complementarity. That is, a net-positive response could still be detected.

Evidence for a neutral (no) relationship:

In some cases, there is no discernible effect of natural enemy species richness on herbivore suppression (Chang 1996, Wilby et al. 2005, Straub and Snyder 2006, Frank et al. 2007). In this condition, a balance between IGP and supplemental herbivore suppression by the intraguild predator may be responsible, but IGP should not be assumed in all cases. Chang (1996) found no evidence for IGP; despite using experimental treatments with combinations of predatory species with IGP potential, behavioral differences between the predators resulted in additive control of the herbivore through resource partitioning. Straub and Snyder (2006) determined that predator identity mattered more than predator species richness; some species were more active predators. Frank et al. (2007) videotaped nocturnal predation encounters of an herbivore species and found that more diverse natural enemy assemblages were more active and attacked prey individuals more frequently than the less diverse assemblage, but they found no difference in herbivore mortality. Thus, a wide range of mechanisms may result in observed neutral relationships between natural enemy diversity and herbivore suppression.

A recent review by Letourneau et al. (2009) demonstrates that the above three scenarios are supported by the accumulated body of tests, yet their meta-analysis using 266 tests yielded an overall positive relationship between enemy diversity and herbivore suppression, particularly in agricultural settings. This general finding supports the potential for taxonomic diversity of natural enemies to indicate herbivore suppression in more cases than not—consistent with the view held by central coast organic farmers. Whether diversity of natural enemies serves as a good predictor of biological control of crop pests in a particular case, however, requires testing, however.

To test whether biodiversity of the wasp family Ichneumonidae, a highly species rich taxon known to contain parasitoids of many crop pests, could serve as an indicator for the biological control of a target pest in annual cropping systems, I sampled Ichneumonidae species richness within farm fields and measured parasitism of sentinel cabbage loopers, *Trichoplusia ni*. In essence, these are two types of indicators of biological control function, with an assumption that they should be correlated measures. Additionally, I tested whether species richness of the subfamily Campopleginae, which contains species known to attack *T. ni*, can be used as an indicator taxon. Because determining species richness within these groups is challenging, requiring extensive training and tools that are impractical in a field environment (i.e., microscopic magnification), it would not be a practical assessment tool for farmers making pest management decisions until DNA detection methods are refined for use in the field. To test the more practical question of whether abundance counts of Ichneumonidae or Campopleginae—assessments that could be conducted with less training and a hand lens—could be used as an indicator of biological control function, I test for a relationship between Ichneumonidae and Campopleginae abundance counts and sentinel-species parasitism. These are important tests as it is often assumed by local farmers that the presence of Ichneumonidae will ensures some amount of pest control, a view supported by generic statements in common biological control information resources, such as the University of California's Statewide Integrated Pest Management Program (2007).

Methods

Study region and research sites

The central coast region of California is a mosaic of natural vegetation (including wetlands, chaparral, oak woodlands, coniferous forest, coastal prairies), farming operations, and urban development. Annual cropping systems dominate the agricultural facets of this mosaic, and the three counties included in this study (Santa Cruz, Monterey and San Benito), account for 16% of the national and 28% of the Californian market value for vegetables, melons, potatoes, and sweet potatoes (USDA

2009); this dominance is stronger for cole and lettuce crops. These three counties are also among the national leaders in organic vegetable production acres (CCOF 2008, USDA 2008). The 25 farms that participated as our research sites are situated in landscapes that encompass the range region’s range from predominantly agricultural, to mixed vegetation-landuse, to predominantly native vegetation. These farms range in size from one to 80 hectares and employ a variety of cultural practices, but produce a similar suite of annual crops and meet National Organic Program production standards.

Measuring parasitism of a sentinel pest

In order to measure parasitism activity at multiple sites and on multiple occasions, where the variety and abundances of crop pests varied over space, time and cultural practices, I used *Trichoplousia ni* as a sentinel pest. *T. ni* larvae are a suitable sentinel because they are a common, low-level pest of cole crops in central coast vegetable fields and are known to host several parasitic wasp and fly species (Flint 1990) but are not highly mobile. To measure parasitoid activity, I exposed *T. ni* larvae, hosted on potted collard (*Brassica oleracea*) plants placed within production farm fields, to local parasitoids in May and September 2007.

Prior to field exposure, *T. ni* eggs were placed on greenhouse grown, potted, collard plants inside individual fine mesh exclosures to prevent pre-experiment parasitism of emerging larvae. After two days, ten plants in one gallon pots containing first instar larvae were placed at 28 sites and left for seven exposure days.

Twelve second to fourth instar *T. ni* larvae were haphazardly collected from each plant at the end of the exposure period, for a total of 120 larvae per site, and reared on artificial diet in a growth chamber at 27°C with a 16:8 day-night cycle. Percent parasitism per plant was determined as the number of parasitized larvae (parasitoid emerged or immature parasitoid detected in dead larvae) divided by the total number of larvae collected per plant. Missing values (e.g., large-scale mortality due to Bt-pesticide application by farm staff at one site and unusually high spider predation at others, which resulted in collection of fewer than 120 larvae) were not included because parasitism of these larvae prior to their death cannot be determined. Site parasitism level was the mean of all ten plant means.

Measuring parasitoid diversity

To measure the diversity of Ichneumonidae visiting central coast farms and potentially attacking *T. ni* or other lepidopteran pests, I collected 48-hour Malaise trap samples in August 2004 and May, July, and August of 2005 and 2006. Use of Malaise-style traps is an effective means of sampling large numbers and diversity of Hymenoptera and other flying insects (Darling and Packer 1988, Fraser et al. 2008) and allows collection of insects during flight, regardless of wind direction. Dark green traps (BioQuip model 2875AG), which work better than the standard white-top design in open, sunny conditions (Townes 1972), were erected at the center each site, or if farming operations made the center unavailable, then in adjacent sections of the field within 50m. Flexibility in sampling location was required due to overhead irrigation and mechanical cultivation timing, and changing crop type throughout the season. Communication with farm management minimized the likelihood that either a) a sample would be affected by these factors or b) a trap would impede their normal farm operations. Trapping positions were selected to keep crop type as consistent as possible across all farms with the following priority ranks: cole crops (*Brassica oleracea*), then lettuce (*Lactuca sativa*) varieties, and finally other vegetable crops.

Ichneumonidae samples were stored in 70% ethanol solution. Individual specimens were removed, dried, and either pinned or point-mounted (depending on body size), and labeled with acquisition data to build a reference collection. I identified Ichneumonidae to subfamily based on Wahl and Sharkey (1993). Specimens within each subfamily were grouped into morphologically distinct "morphospecies" (Oliver and Beattie 1996, Skillen et al. 2000) categories –drawing on generic keys for guidance when available (Townes 1969), in consultation with Dr. Nicholas Mills (*personal communications*), and our detailed descriptions distinguishing among similar morphs (A2). We recorded abundances of each morphospecies per sample. For both total Ichneumonidae and for the subfamily Campopleginae, we calculated abundance and species richness based on the 7-sample cumulative data set.

Data analysis

To test whether species richness of local Ichneumonidae captures are positively associated with parasitism of *T. ni*, I conducted correlations in PC-SAS version 9.2 (SAS 2003). I used the same approach to test for relationships between each of Campopleginae diversity, Ichneumonidae abundance, and Campopleginae abundance with parasitism levels. I additionally used correlations to test whether parasitism by the dominant parasitoid of *T. ni* is positively associated with these higher order taxa, and whether Malaise captures of that dominant parasitoid are positively associated with parasitism of *T. ni.*

Results

There was no relationship between the abundance of Ichneumonidae captured in Malaise samples and parasitism of *T. ni* larvae ($R^2 = 0.0225$, $p = 0.474$, Fig. 3.1a). Similarly, there was no relationship between campoplegine abundance and parasitism ($R^2 = 0.0474$, $p = 0.2961$, Fig. 3.1b). Thus simple counts at either taxonomic level cannot be used to indicate parasitism activity on nearby *T. ni* larvae. Abundance of the dominant ichneumonid parasitoid, *H. exiguae*, was not associated with *T. ni* parasitism ($R^2 = 0.0562$, $p = 0.2541$, Fig. 3.1c). Abundance of *H. exiguae* was marginally positively associated with abundance of Campopleginae ($R^2 = 0.1216$, $p = 0.0547$, Fig. 1.3d) although this pattern is driven by one high value for *H. exiguae* abundance. *H. exiguae* abundance was not related to Ichneumonidae abundance ($R^2 = 0.0024$, $p = 0.7942$, Fig. 1.3e).

The lack of correspondence between abundance of *H. exiguae* and its subfamily taxon and between the abundance of *H. exiguae* and parasitism of *T. ni* was surprising. Because *H. exiguae* represents only eight percent of campoplegine captures from our Malaise samples, we checked whether the lack of correlations was due to a lack of statistical power with our sample size of N=25. I conducted post hoc power analyses using SAS 9.2, setting power at 0.80 and alpha at 0.05. Power analyses of parasitism correlation values showed that sample sizes would have to increase up to N= 137, 163, and 346 for *H. exiguae*, Campopleginae, and Ichneumonidae abundances, respectively, in order for the observed correlation values to reach statistical significance. The power analyses suggest that the positive slopes resulting from these correlations are very small compared to the variances (Fig. 3.1a-e) and are unlikely to be biologically important. Similarly, I found no relationship between species richness of either Ichneumonidae or Campopleginae captured and the percentage of larvae parasitized (Ichneumonidae $R^2 = 0.0008$, $p = 0.887$; Campopleginae $R^2 = 0.0159$, $p = 0.5393$).

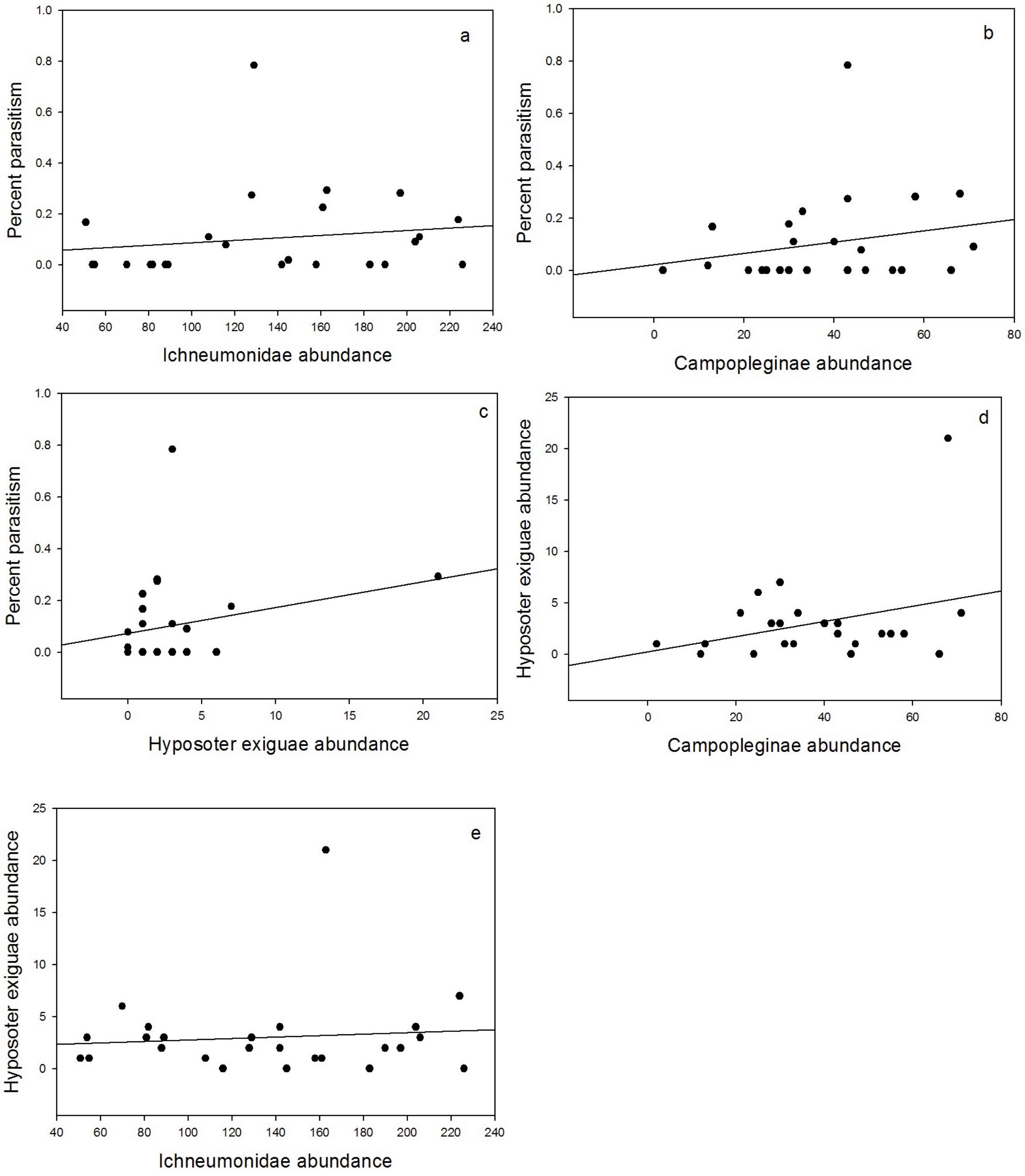


Figure 3.1. Relationships between potential indicator taxa (a) Ichneumonidae abundance, (b) Campopleginae abundance, and (c) *H. exiguae* abundance and percent of sentinel *T. ni* larve parasitized, and relationships between (d) Campopleginae

abundance and (e) Ichneumonidae abundance and *H. exiguae* abundance from Malaise trap captures.

Discussion

Two theoretically likely indicator taxa (family and subfamily containing the dominant parasitoid) sampled repeatedly over three years were unrelated to parasitism of a sentinel pest in the following year. These two higher taxon groups were logical candidates to test for association with *H. exiguae* because close relatives should have similar habitat requirements and because it is impractical to sample wasps at the species level. However these logical criteria fall short when the distribution of species providing an ecological service is not in concert with that of the larger group. Ichneumonidae is a highly diverse family, with an estimated 60,000species (Wahl and Sharkey 1993), and Campopleginae is a relatively diverse subfamily (the third most species rich of 14 subfamilies collected in this study, with 13 morphospecies; see Table 1.3). Host specificity (Shaw 2006) and host taxon segregation among some subfamilies (Wahl and Sharkey 1993), suggest using caution about assumptions of habitat similarity between a particular species and a higher taxonomic level, particularly for species-rich taxa.

Abundance measures, in particular, would have been practical for farmers or researchers with basic entomological knowledge. Test results for campoplegine abundance as an indicator, demonstrating only a weak positive association with *H. exiguae* abundance and no association with parasitism, is surprising because the subfamily is more homogenous in host taxon usage, containing many parasitoids of Lepidoptera, including several well known crop pests aside from *T. ni*. A more comprehensive test of Campopleginae as an indicator taxon, including more lepidopteran pest species, would more robustly either validate the assumption of positive relationship between Ichneumonidae and pest control (as currently supported by UC IPM 2007) or discard it, rather by the results of this single species-based test. For example, a survey of the variety of the lepidopteran pests present in mixed vegetable fields, measuring rates of parasitism they experience naturally rather than in sentinel tests, and testing for associations between that more general parasitism measure and Campoplegine abundance would be a more direct test of biocontrol service. Having a more definitive answer to this question would be a helpful resource to farmers and pest control advisers.

If selection (with testing) of indicator taxa and their use in forestry and agriculture surveys is our present approach for measuring environmental health and ecological functions, the future is likely to be based on a further removed proxies. Dung beetles (Scarabidae: Coleoptera) have been used as indicators of biodiversity (due to their reliance on the presence of other fauna) and forest health (due to their role as decomposers), and because they are accepted for satisfying forest management certification surveys (Aguilar-Amuchastegui and Henebry 2007). In an effort to replace dung beetle surveys—while less difficult and costly than comprehensive biodiversity inventories, is still labor-intensive—Aguilar-Amuchastegui and Henebry (2007) evaluated remote sensing of logging intensity as an indicator of dung beetle diversity with positive results. In an agricultural context, Paoletti et al. (1999) tested the indicator value of farmscape-level features to represent the diversity of beneficial insects that provide ecological services to agriculture; what they did not test was the appropriateness of the mixed-level (families and orders) arthropod taxa they selected as indicators for the desired ecological benefits. As levels of abstraction are added between indicators and targets, in which each added level is less likely to represent our goal targets as accurately as the next closer-level indicator, the importance of demonstrating indicator value at each level grows. There may well be measurable relationships between remotely sensed habitat characteristics and the diversity (or abundances) of taxa we believe are appropriate indicators of ecological functions. However, without testing the quality of these intermediate indicator taxa, we will not know whether our remotely sensed, abstracted proxies are helping us conserve real function on the ground.

APPENDIX 1

LANDSCAPE CHARACTERIZATION

Methods

The geographic extent of the 35 sites required using both State plane 3 (Santa Cruz and San Benito counties) and 4 (Monterey county) projections. To obtain complete photographic coverage of all landscapes, we used four different qualities of digitally orthorectified photographs: color, infrared, and black and white photographs at 0.1524 m resolution, and color photographs at 0.6096 m resolution. To build landscape maps, we calculated the mean center of each site, and drew both 1.5km (7.07 km^2) and 0.5km (0.785 km^2) buffers from the mean centers to designate larger and smaller landscape scales. Thies et al. (2003) found that patterns of attack by Ichneumonidae in Germany were most strongly associated with vegetation characteristics at a scale of 1.5km radius, among radial lengths tested ranging from 0.5 to 6.0km. Also in Germany, van Nouhuys and Hanski (2002) found that while *Cotesia* (Braconidae: Microgastrinae) movement was affected by vegetation and host density features at 0.5km, *Hypososter* (Ichneumonidae: Campopleginae) dispersal limitation existed appeared to be close to 1.6km. These two parasitoid families were responsible for most of the parasitization of the sentinel *T. ni* larva in this investigation.

We manually digitized boundaries between different landcover classes (based on hue, brightness, and texture) covering the entire large buffer area to generate landcover polygons. We used a minimum mapping unit of 50m x 50m, with the exception of trees located within annual crop fields –thereby representing the only perennial vegetation in some annual crop areas—which we did digitize. Through a stratified methodology, we interpreted aerial photograph coverages for each polygon to assign landuse and vegetation classes. That is, we first attributed landuse class names, which were designated based on likely habitat quality for parasitic Hymenoptera, to the polygons not dominated by vegetative cover. For example, higher landcover of paved roads in a given polygon should indicate a relatively hostile environment due to lack of the habitat requirements as well as increased likelihood of mortality due to impact with cars. Paved road, gravel road, industrial, commercial, and residential landuse classes can be considered a gradient of decreasing environmental hostility to Hymenoptera with decreasing impervious and increasing vegetative cover. In our second level of attribution, we assigned vegetation classes to the remaining polygons. This process relied on extensive pre-attribution development of vegetation class visual characteristics, for which we developed a photographic library. Vegetation mixes were denoted by dominant taxa in order of their prominence, such as oak-conifer, considering all taxa with greater than 10 percent coverage within the polygon; this yielded several 3-taxa vegetation classes.

To ground-truth the quality of this data set, we first summed the landcover across all 35 landscapes by vegetation or landuse class. Among the vegetation classes only, we selected 200 points stratified by class based on proportional coverage area, but assigned points randomly within each class. Among the landuse classes, we used the same procedure to assign 100 stratified-random points. Using hand-held GPS units, we then visited each of the 300 points to verify the vegetation or landuse class attributed within the GIS, and found we had an 89% accuracy rate. Attribution errors were primarily cases of ambiguous hue and pattern distinctions, such as sometimes occurs between *Quercus* and *Salix* designations.

Results

Here, we report coverages for 44 separate vegetation and landuse classes, five "composite" vegetation classes (combined based on dominant vegetation due to rarity of some classes), as well as four additional combination variables: total vegetation (veg), vegetation class richness (numveg), and coverage of both perennial and annual vegetation (pernveg, annveg), for our 34 research sites at both the larger (1.5km radius, 7.07 km^2) (Table A1a) and smaller (0.5km radius, 0.785 km^2) (Table A1b) landscape scales.

Vegetative and landuse names (and abbreviations, when used) are: *Acacia*, *Alnus* (alder), annual crop (anncrp), *Laurus* (bay), *Rubus* (blkbry), coastal scrub (coastscb), *Rhamnus* (coff, coffee), *Baccharis* (coy, coyot), umbellifer hemlock (hem, hemlk), *Salvia* (sage), commercial (commrcl), conifer, grass, *Eucalpytus* (euc), freshwater (freshw), *Raphanus* (rad), gravel roads (gravel), hedgerow (hedgrw), *Carpobrotus* (iceplnt), industrial (indust), *Arctostaphylos* (manz), *Acer* (maple), marsh, *Quercus* (oak), ocean, park, paved roads, perennial crop (prncrp), *Toxicodendron* (poisnoak), rail line, residential, rural, *Lithocarpus* (tanoak), and *Salix* (willow).

Table A1a. Large (1.5km radius) landscape scale coverages as fractions of total area

site	acacia	Alder	anncrp	bay	blkbry	coastscb	coffcomp	coffee	coffcoy	coffhem	coffsagecoy	commrcl	conifer
1	0.0000	0.0000	0.9034	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0012
2	0.0000	0.0169	0.0915	0.0000	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0086	0.0630
3	0.0000	0.0000	0.2160	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0328	0.0157
4	0.0063	0.0000	0.0100	0.0184	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0780	0.1249
5	0.0000	0.0000	0.0469	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0085	0.0632
6	0.0000	0.0028	0.0509	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0070	0.1397
7	0.0000	0.0070	0.1376	0.0013	0.0042	0.0306	0.0050	0.0005	0.0045	0.0000	0.0000	0.0000	0.0290
8	0.0000	0.0000	0.3206	0.0000	0.0009	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0236	0.0030
9	0.0000	0.0000	0.6675	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0961	0.0021
10	0.0000	0.0000	0.1490	0.0000	0.0054	0.0047	0.0007	0.0000	0.0007	0.0000	0.0000	0.0497	0.0085
11	0.0000	0.0227	0.0423	0.0000	0.0000	0.0051	0.0000	0.0000	0.0000	0.0000	0.0000	0.0007	0.2079
12	0.0000	0.0000	0.2659	0.0000	0.0005	0.0000	0.0028	0.0000	0.0028	0.0000	0.0000	0.0011	0.0258
13	0.0000	0.0000	0.0093	0.0056	0.0035	0.0000	0.0001	0.0000	0.0001	0.0000	0.0000	0.0146	0.0797
14	0.0000	0.0000	0.0073	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.6632
15	0.0000	0.0000	0.3195	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0006
16	0.0000	0.0000	0.4805	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0007
17	0.0000	0.0000	0.7117	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0055	0.0007
18	0.0000	0.0000	0.6980	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0064
19	0.0000	0.0000	0.3909	0.0000	0.0007	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002
20	0.0000	0.0000	0.1108	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002
21	0.0000	0.0308	0.0258	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.8144
22	0.0000	0.0226	0.0258	0.0000	0.0000	0.0014	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.5554
23	0.0112	0.0000	0.0100	0.0297	0.0008	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0662	0.2001
24	0.0000	0.0000	0.6818	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0046	0.0000
25	0.0000	0.0000	0.4236	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0142	0.0060
26	0.0000	0.0000	0.0214	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0119	0.0213
27	0.0000	0.0000	0.0474	0.0006	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0119	0.0599
28	0.0000	0.0000	0.7966	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0047
29	0.0000	0.0059	0.2611	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0142	0.0253
30	0.0000	0.0000	0.3285	0.0000	0.0037	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
31	0.0003	0.0000	0.2113	0.0000	0.0017	0.0253	0.0004	0.0004	0.0000	0.0000	0.0000	0.0000	0.0384
32	0.0000	0.0073	0.0516	0.0009	0.0027	0.0123	0.0208	0.0051	0.0000	0.0021	0.0136	0.0000	0.0536
33	0.0000	0.0000	0.0093	0.0177	0.0011	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0386	0.0925
34	0.0000	0.0002	0.2455	0.0000	0.0007	0.0057	0.0058	0.0006	0.0052	0.0000	0.0000	0.0049	0.0101

Table A1a. Large (1.5km radius) landscape scale coverages as fractions of total area

site	coycomp	coyot	coyotgrass	coyothem	euc	freshw	grasscomp	grass	grasscoyot	grassrad	gravel	hedgrw
1	0.0000	0.0000	0.0000	0.0000	0.0049	0.0018	0.0134	0.0104	0.0000	0.0030	0.0006	0.0007
2	0.0279	0.0279	0.0000	0.0000	0.0584	0.0161	0.1826	0.1743	0.0000	0.0083	0.0037	0.0000
3	0.0515	0.0515	0.0000	0.0000	0.0378	0.0009	0.2580	0.2087	0.0000	0.0493	0.0016	0.0009
4	0.0058	0.0058	0.0000	0.0000	0.0142	0.0061	0.1553	0.1508	0.0000	0.0045	0.0030	0.0000
5	0.1572	0.1572	0.0000	0.0000	0.0015	0.0085	0.1210	0.0979	0.0000	0.0231	0.0094	0.0000
6	0.1480	0.1480	0.0000	0.0000	0.0000	0.0093	0.1670	0.1571	0.0000	0.0099	0.0047	0.0000
7	0.0985	0.0736	0.0000	0.0249	0.0012	0.0052	0.2378	0.2311	0.0000	0.0067	0.0046	0.0003
8	0.0247	0.0236	0.0000	0.0011	0.0146	0.0449	0.2336	0.2244	0.0000	0.0092	0.0264	0.0001
9	0.0026	0.0026	0.0000	0.0000	0.0000	0.0137	0.0457	0.0405	0.0000	0.0052	0.0056	0.0000
10	0.0307	0.0253	0.0000	0.0054	0.0231	0.0069	0.2103	0.1875	0.0102	0.0125	0.0171	0.0001
11	0.1807	0.1807	0.0000	0.0000	0.0022	0.0027	0.2910	0.2729	0.0000	0.0181	0.0225	0.0000
12	0.0058	0.0058	0.0000	0.0000	0.0279	0.0340	0.2139	0.2128	0.0000	0.0012	0.0043	0.0005
13	0.0203	0.0190	0.0000	0.0012	0.0244	0.0004	0.4778	0.4731	0.0020	0.0027	0.0067	0.0002
14	0.2075	0.2075	0.0000	0.0000	0.0000	0.0000	0.0704	0.0555	0.0068	0.0080	0.0191	0.0000
15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0158	0.3019	0.2920	0.0000	0.0099	0.0113	0.0000
16	0.0000	0.0000	0.0000	0.0000	0.0002	0.0019	0.3904	0.3834	0.0000	0.0070	0.0198	0.0000
17	0.0000	0.0000	0.0000	0.0000	0.0000	0.0022	0.2007	0.1858	0.0000	0.0149	0.0122	0.0000
18	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002	0.1037	0.0884	0.0000	0.0153	0.0068	0.0000
19	0.0039	0.0039	0.0000	0.0000	0.0000	0.0014	0.3370	0.3322	0.0000	0.0048	0.0080	0.0024
20	0.0000	0.0000	0.0000	0.0000	0.0022	0.0033	0.8085	0.8062	0.0000	0.0022	0.0012	0.0001
21	0.0471	0.0471	0.0000	0.0000	0.0000	0.0050	0.0174	0.0174	0.0000	0.0000	0.0030	0.0000
22	0.0393	0.0393	0.0000	0.0000	0.0000	0.0039	0.0310	0.0310	0.0000	0.0000	0.0045	0.0000
23	0.0045	0.0045	0.0000	0.0000	0.0164	0.0063	0.0937	0.0897	0.0000	0.0040	0.0032	0.0000
24	0.0052	0.0052	0.0000	0.0000	0.0266	0.0000	0.0576	0.0551	0.0000	0.0024	0.0047	0.0000
25	0.0137	0.0137	0.0000	0.0000	0.0037	0.0245	0.2804	0.2519	0.0000	0.0285	0.0007	0.0000
26	0.2126	0.2126	0.0000	0.0000	0.0013	0.0037	0.1608	0.1301	0.0000	0.0307	0.0042	0.0000
27	0.1508	0.1508	0.0000	0.0000	0.0015	0.0075	0.1226	0.0929	0.0000	0.0297	0.0098	0.0000
28	0.0045	0.0045	0.0000	0.0000	0.0000	0.0702	0.0309	0.0185	0.0000	0.0124	0.0088	0.0004
29	0.0155	0.0155	0.0000	0.0000	0.0000	0.0238	0.3066	0.3057	0.0000	0.0008	0.0212	0.0000
30	0.0226	0.0226	0.0000	0.0000	0.0000	0.0114	0.2424	0.2394	0.0000	0.0030	0.0220	0.0000
31	0.1227	0.1205	0.0000	0.0022	0.0025	0.0051	0.2283	0.2086	0.0000	0.0197	0.0123	0.0000
32	0.2274	0.1940	0.0000	0.0333	0.0055	0.0010	0.2101	0.2084	0.0000	0.0017	0.0051	0.0000
33	0.0064	0.0064	0.0000	0.0000	0.0196	0.0020	0.4055	0.4046	0.0000	0.0008	0.0046	0.0002
34	0.0474	0.0282	0.0005	0.0187	0.0268	0.0015	0.1436	0.1246	0.0166	0.0024	0.0012	0.0003

Table A1a. Large (1.5km radius) landscape scale coverages as fractions of total area

site	hemlk	iceplnt	indust	manz	maple	marsh	oakcomp	oak	oakbay	oakconfr	oakgrass	ocean
1	0.0000	0.0002	0.0603	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
2	0.0003	0.0005	0.0074	0.0000	0.0000	0.0000	0.1835	0.1471	0.0000	0.0364	0.0000	0.0000
3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0047	0.2293	0.2293	0.0000	0.0000	0.0000	0.0000
4	0.0016	0.0013	0.0589	0.0000	0.0047	0.0014	0.1706	0.0629	0.0802	0.0275	0.0000	0.0000
5	0.0000	0.0000	0.0018	0.0000	0.0015	0.0000	0.2854	0.2836	0.0000	0.0018	0.0000	0.0000
6	0.0043	0.0000	0.0044	0.0000	0.0003	0.0000	0.1585	0.1585	0.0000	0.0000	0.0000	0.0000
7	0.0183	0.0000	0.0026	0.0000	0.0000	0.0043	0.0705	0.0461	0.0209	0.0013	0.0022	0.2706
8	0.0000	0.0061	0.0000	0.0000	0.0000	0.1095	0.0194	0.0194	0.0000	0.0000	0.0000	0.0000
9	0.0000	0.0213	0.0082	0.0000	0.0000	0.0504	0.0054	0.0054	0.0000	0.0000	0.0000	0.0000
10	0.0014	0.0037	0.0402	0.0000	0.0000	0.0016	0.0265	0.0244	0.0003	0.0017	0.0000	0.1823
11	0.0047	0.0000	0.0000	0.0000	0.0031	0.0112	0.0298	0.0298	0.0000	0.0000	0.0000	0.1176
12	0.0001	0.0000	0.0419	0.0000	0.0000	0.0082	0.0599	0.0469	0.0000	0.0131	0.0000	0.0000
13	0.0006	0.0000	0.0081	0.0000	0.0000	0.0006	0.1057	0.0873	0.0000	0.0184	0.0000	0.0000
14	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0281	0.0059	0.0000	0.0222	0.0000	0.0000
15	0.0000	0.0000	0.0143	0.0000	0.0057	0.0171	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
16	0.0000	0.0000	0.0508	0.0000	0.0000	0.0000	0.0001	0.0001	0.0000	0.0000	0.0000	0.0000
17	0.0000	0.0000	0.0161	0.0000	0.0000	0.0000	0.0011	0.0011	0.0000	0.0000	0.0000	0.0000
18	0.0000	0.0000	0.0335	0.0000	0.0000	0.0001	0.0003	0.0003	0.0000	0.0000	0.0000	0.0000
19	0.0007	0.0000	0.0329	0.0000	0.0000	0.0069	0.0012	0.0012	0.0000	0.0000	0.0000	0.0000
20	0.0000	0.0000	0.0038	0.0000	0.0000	0.0428	0.0037	0.0037	0.0000	0.0000	0.0000	0.0000
21	0.0000	0.0000	0.0000	0.0000	0.0038	0.0066	0.0000	0.0000	0.0000	0.0000	0.0000	0.0195
22	0.0000	0.0084	0.0105	0.0000	0.0038	0.0086	0.0000	0.0000	0.0000	0.0000	0.0000	0.2423
23	0.0013	0.0014	0.0584	0.0000	0.0047	0.0008	0.1749	0.0758	0.0603	0.0389	0.0000	0.0000
24	0.0003	0.0000	0.1180	0.0000	0.0000	0.0017	0.0227	0.0227	0.0000	0.0000	0.0000	0.0000
25	0.0008	0.0000	0.0019	0.0000	0.0000	0.1310	0.0500	0.0500	0.0000	0.0000	0.0000	0.0000
26	0.0000	0.0000	0.0030	0.0000	0.0006	0.0000	0.2697	0.2697	0.0000	0.0000	0.0000	0.0000
27	0.0000	0.0000	0.0007	0.0000	0.0014	0.0000	0.2897	0.2879	0.0000	0.0018	0.0000	0.0000
28	0.0000	0.0000	0.0128	0.0000	0.0000	0.0209	0.0052	0.0052	0.0000	0.0000	0.0000	0.0000
29	0.0000	0.0000	0.0021	0.0000	0.0000	0.0149	0.1866	0.1658	0.0000	0.0208	0.0000	0.0000
30	0.0000	0.0000	0.0119	0.0210	0.0000	0.0015	0.1765	0.1765	0.0000	0.0000	0.0000	0.0000
31	0.0306	0.0004	0.0289	0.0000	0.0000	0.0043	0.0408	0.0253	0.0000	0.0155	0.0000	0.2067
32	0.0151	0.0000	0.0188	0.0000	0.0000	0.0000	0.0519	0.0238	0.0051	0.0230	0.0000	0.2106
33	0.0010	0.0000	0.0105	0.0000	0.0000	0.0000	0.0862	0.0570	0.0292	0.0000	0.0000	0.0000
34	0.0062	0.0091	0.0096	0.0000	0.0000	0.0000	0.0856	0.0823	0.0000	0.0000	0.0034	0.2277

Table A1a. Large (1.5km radius) landscape scale coverages as fractions of total area

site	park	pavedroad	prncrp	poisnoak	railline	resid	rural	sagecomp	sage	sagehemcoy	tanoak	willow
1	0.0000	0.0079	0.0000	0.0000	0.0000	0.0037	0.0000	0.0000	0.0000	0.0000	0.0000	0.0018
2	0.0047	0.0129	0.1793	0.0022	0.0000	0.0427	0.0633	0.0000	0.0000	0.0000	0.0000	0.0337
3	0.0000	0.0086	0.0051	0.0028	0.0000	0.0997	0.0149	0.0000	0.0000	0.0000	0.0000	0.0198
4	0.0408	0.0308	0.0038	0.0000	0.0000	0.2432	0.0041	0.0000	0.0000	0.0000	0.0000	0.0152
5	0.0395	0.0137	0.0007	0.0000	0.0000	0.1056	0.0158	0.0891	0.0891	0.0000	0.0000	0.0292
6	0.1302	0.0265	0.0002	0.0000	0.0000	0.0745	0.0009	0.0370	0.0370	0.0000	0.0000	0.0336
7	0.0021	0.0087	0.0000	0.0031	0.0027	0.0134	0.0000	0.0238	0.0122	0.0117	0.0000	0.0174
8	0.0000	0.0097	0.0006	0.0005	0.0000	0.0139	0.0500	0.0000	0.0000	0.0000	0.0000	0.0979
9	0.0000	0.0555	0.0004	0.0000	0.0000	0.0108	0.0007	0.0000	0.0000	0.0000	0.0000	0.0140
10	0.0084	0.0139	0.0008	0.0005	0.0028	0.1637	0.0000	0.0044	0.0000	0.0044	0.0000	0.0438
11	0.0000	0.0076	0.0039	0.0000	0.0001	0.0028	0.0047	0.0000	0.0000	0.0000	0.0000	0.0368
12	0.0087	0.0361	0.0387	0.0053	0.0000	0.1683	0.0000	0.0000	0.0000	0.0000	0.0010	0.0492
13	0.0000	0.0171	0.0017	0.0000	0.0000	0.1854	0.0007	0.0029	0.0000	0.0029	0.0000	0.0347
14	0.0000	0.0000	0.0005	0.0000	0.0000	0.0003	0.0038	0.0000	0.0000	0.0000	0.0000	0.0000
15	0.0000	0.0069	0.2204	0.0000	0.0000	0.0204	0.0265	0.0000	0.0000	0.0000	0.0000	0.0395
16	0.0000	0.0212	0.0208	0.0000	0.0000	0.0000	0.0136	0.0000	0.0000	0.0000	0.0000	0.0000
17	0.0000	0.0044	0.0147	0.0000	0.0030	0.0025	0.0000	0.0000	0.0000	0.0000	0.0000	0.0252
18	0.0000	0.0203	0.0878	0.0000	0.0000	0.0025	0.0114	0.0000	0.0000	0.0000	0.0000	0.0289
19	0.0000	0.0095	0.1854	0.0000	0.0000	0.0100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0089
20	0.0000	0.0042	0.0000	0.0019	0.0000	0.0030	0.0143	0.0000	0.0000	0.0000	0.0000	0.0000
21	0.0000	0.0000	0.0021	0.0000	0.0000	0.0008	0.0050	0.0000	0.0000	0.0000	0.0000	0.0186
22	0.0000	0.0028	0.0021	0.0000	0.0000	0.0149	0.0065	0.0000	0.0000	0.0000	0.0000	0.0162
23	0.0601	0.0332	0.0038	0.0000	0.0000	0.2004	0.0060	0.0000	0.0000	0.0000	0.0000	0.0128
24	0.0031	0.0274	0.0009	0.0010	0.0023	0.0400	0.0000	0.0000	0.0000	0.0000	0.0000	0.0020
25	0.0000	0.0059	0.0009	0.0000	0.0000	0.0122	0.0000	0.0000	0.0000	0.0000	0.0000	0.0302
26	0.0174	0.0123	0.0009	0.0000	0.0000	0.1890	0.0089	0.0233	0.0233	0.0000	0.0000	0.0373
27	0.0287	0.0125	0.0007	0.0000	0.0000	0.1290	0.0190	0.0680	0.0680	0.0000	0.0000	0.0382
28	0.0000	0.0039	0.0000	0.0000	0.0000	0.0053	0.0000	0.0000	0.0000	0.0000	0.0000	0.0357
29	0.0000	0.0103	0.0066	0.0000	0.0000	0.0038	0.0036	0.0517	0.0517	0.0000	0.0000	0.0440
30	0.0069	0.0633	0.0000	0.0004	0.0000	0.0277	0.0000	0.0263	0.0075	0.0187	0.0000	0.0341
31	0.0000	0.0092	0.0005	0.0001	0.0026	0.0016	0.0042	0.0126	0.0126	0.0000	0.0000	0.0093
32	0.0000	0.0064	0.0000	0.0066	0.0041	0.0167	0.0023	0.0595	0.0030	0.0565	0.0000	0.0097
33	0.0000	0.0228	0.0017	0.0000	0.0000	0.2533	0.0000	0.0000	0.0000	0.0000	0.0000	0.0270
34	0.0149	0.0131	0.0002	0.0059	0.0004	0.1089	0.0000	0.0000	0.0000	0.0000	0.0000	0.0246

Table A1a. Large (1.5km radius) landscape

site	veg	numveg	pernveg	annveg
1	0.0220	4	0.0044	0.9168
2	0.5693	10	0.5074	0.2744
3	0.6204	8	0.3259	0.4787
4	0.5201	13	0.3514	0.1683
5	0.7494	11	0.6277	0.1678
6	0.6913	10	0.5202	0.2223
7	0.5524	15	0.2911	0.3980
8	0.5042	10	0.1471	0.6637
9	0.1202	7	0.0246	0.7636
10	0.3615	13	0.1260	0.3623
11	0.7952	11	0.4900	0.3492
12	0.4010	11	0.1900	0.4881
13	0.7560	11	0.2546	0.4883
14	0.9691	4	0.8992	0.0776
15	0.3648	5	0.2663	0.6385
16	0.3916	2	0.0217	0.8709
17	0.2277	4	0.0417	0.9124
18	0.1394	3	0.1234	0.8019
19	0.3619	7	0.2051	0.7355
20	0.8595	5	0.0061	0.9620
21	0.9387	7	0.9168	0.0499
22	0.6783	9	0.6409	0.0654
23	0.5511	13	0.4426	0.1058
24	0.1171	7	0.0319	0.7414
25	0.5160	8	0.1009	0.8358
26	0.7272	10	0.5660	0.1822
27	0.7326	11	0.6092	0.1701
28	0.1024	6	0.0510	0.8484
29	0.6505	11	0.3355	0.5826
30	0.5285	8	0.2846	0.5724
31	0.5173	11	0.2521	0.4745
32	0.6834	14	0.4527	0.2768
33	0.6571	9	0.2331	0.4157
34	0.3629	12	0.1868	0.3954

Table A1b. Small (0.5km radius) landscape scale coverages as fractions of total area

site	acacia	alder	anncrp	bay	blkbry	coastscb	coffcomp	coffee	coffcoy	coffhem	coffsagecoy	commrcl	conifer
1	0.0000	0.0000	0.9733	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0037
2	0.0000	0.0000	0.0688	0.0000	0.0012	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0027	0.0959
3	0.0000	0.0000	0.3656	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0878	0.0406
4	0.0183	0.0000	0.0299	0.0039	0.0030	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1991	0.1348
5	0.0000	0.0000	0.3391	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0377	0.0304
6	0.0000	0.0055	0.0903	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2135
7	0.0000	0.0110	0.2733	0.0000	0.0154	0.0249	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0072
8	0.0000	0.0000	0.3922	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001
9	0.0000	0.0000	0.6036	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1303	0.0077
10	0.0000	0.0000	0.1913	0.0000	0.0028	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1083	0.0135
11	0.0000	0.0743	0.2083	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0607
12	0.0000	0.0000	0.3732	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0071	0.0000
13	0.0000	0.0000	0.0074	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0078
14	0.0000	0.0000	0.0594	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2666
15	0.0000	0.0000	0.3247	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
16	0.0000	0.0000	0.8433	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0031
17	0.0000	0.0000	0.9234	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0078	0.0020
18	0.0000	0.0000	0.9827	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
19	0.0000	0.0000	0.5777	0.0000	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
20	0.0000	0.0000	0.7942	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
21	0.0000	0.0518	0.1161	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.6693
22	0.0000	0.1536	0.1121	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3337
23	0.0072	0.0000	0.0643	0.0299	0.0014	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0131	0.2570
24	0.0000	0.0000	0.6310	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
25	0.0000	0.0000	0.7414	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0051
26	0.0000	0.0000	0.0933	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0379
27	0.0000	0.0000	0.0884	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0039	0.0299
28	0.0000	0.0000	0.7991	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0051
29	0.0000	0.0000	0.3979	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0636
30	0.0000	0.0000	0.8708	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
31	0.0000	0.0000	0.1748	0.0000	0.0073	0.0415	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0039
32	0.0000	0.0000	0.1134	0.0000	0.0026	0.0000	0.0464	0.0000	0.0000	0.0048	0.0415	0.0000	0.0038
33	0.0000	0.0000	0.0701	0.0142	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0089	0.0249
34	0.0000	0.0000	0.4439	0.0000	0.0012	0.0000	0.0055	0.0055	0.0000	0.0000	0.0000	0.0303	0.0194

Table A1b. Small (0.5km radius) landscape scale coverages as fractions of total area

site	coycomp	coyot	coyotgrass	coyothem	euc	freshw	grasscomp	grass	grasscoyot	grassrad	gravel	hedgrw
1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0045	0.0000	0.0000	0.0045	0.0000	0.0000
2	0.0196	0.0196	0.0000	0.0000	0.0981	0.0316	0.2462	0.2375	0.0000	0.0086	0.0020	0.0000
3	0.0535	0.0535	0.0000	0.0000	0.0000	0.0000	0.1587	0.0769	0.0000	0.0819	0.0000	0.0078
4	0.0028	0.0028	0.0000	0.0000	0.0076	0.0106	0.1743	0.1737	0.0000	0.0007	0.0042	0.0000
5	0.0004	0.0004	0.0000	0.0000	0.0107	0.0107	0.0636	0.0607	0.0000	0.0029	0.0259	0.0000
6	0.1176	0.1176	0.0000	0.0000	0.0000	0.0204	0.0712	0.0522	0.0000	0.0190	0.0000	0.0000
7	0.0431	0.0078	0.0000	0.0353	0.0018	0.0053	0.3608	0.3595	0.0000	0.0013	0.0104	0.0024
8	0.0006	0.0006	0.0000	0.0000	0.0057	0.0591	0.2305	0.2305	0.0000	0.0000	0.0000	0.0008
9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0165	0.0104	0.0000	0.0061	0.0016	0.0000
10	0.0427	0.0342	0.0000	0.0085	0.0094	0.0239	0.2534	0.2226	0.0203	0.0104	0.0015	0.0005
11	0.1479	0.1479	0.0000	0.0000	0.0000	0.0003	0.3490	0.3404	0.0000	0.0085	0.0037	0.0000
12	0.0000	0.0000	0.0000	0.0000	0.0228	0.0000	0.2860	0.2825	0.0000	0.0036	0.0089	0.0000
13	0.0000	0.0000	0.0000	0.0000	0.0402	0.0000	0.3670	0.3670	0.0000	0.0000	0.0269	0.0000
14	0.4319	0.4319	0.0000	0.0000	0.0000	0.0000	0.1958	0.1852	0.0106	0.0000	0.0051	0.0000
15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0991	0.1981	0.1876	0.0000	0.0105	0.0182	0.0000
16	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1177	0.1009	0.0000	0.0168	0.0001	0.0000
17	0.0000	0.0000	0.0000	0.0000	0.0000	0.0033	0.0155	0.0000	0.0000	0.0155	0.0004	0.0000
18	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0036	0.0000	0.0000	0.0036	0.0000	0.0000
19	0.0000	0.0000	0.0000	0.0000	0.0000	0.0054	0.0229	0.0161	0.0000	0.0068	0.0000	0.0179
20	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1310	0.1302	0.0000	0.0008	0.0018	0.0013
21	0.0602	0.0602	0.0000	0.0000	0.0000	0.0094	0.0130	0.0130	0.0000	0.0000	0.0022	0.0000
22	0.0918	0.0918	0.0000	0.0000	0.0000	0.0138	0.1160	0.1160	0.0000	0.0000	0.0113	0.0000
23	0.0029	0.0029	0.0000	0.0000	0.0002	0.0148	0.0779	0.0763	0.0000	0.0015	0.0039	0.0000
24	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0652	0.0604	0.0000	0.0048	0.0163	0.0000
25	0.0000	0.0000	0.0000	0.0000	0.0000	0.0036	0.2392	0.2038	0.0000	0.0354	0.0000	0.0000
26	0.1149	0.1149	0.0000	0.0000	0.0115	0.0075	0.1552	0.1225	0.0000	0.0327	0.0113	0.0000
27	0.0518	0.0518	0.0000	0.0000	0.0132	0.0132	0.0765	0.0765	0.0000	0.0000	0.0136	0.0000
28	0.0025	0.0025	0.0000	0.0000	0.0000	0.0698	0.0106	0.0106	0.0000	0.0000	0.0087	0.0000
29	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.3728	0.3728	0.0000	0.0000	0.0139	0.0000
30	0.0131	0.0131	0.0000	0.0000	0.0000	0.0000	0.0692	0.0692	0.0000	0.0000	0.0008	0.0000
31	0.1474	0.1474	0.0000	0.0000	0.0000	0.0224	0.3151	0.2773	0.0000	0.0378	0.0220	0.0000
32	0.0947	0.0439	0.0000	0.0508	0.0000	0.0005	0.4514	0.4514	0.0000	0.0000	0.0029	0.0000
33	0.0000	0.0000	0.0000	0.0000	0.0368	0.0000	0.5828	0.5828	0.0000	0.0000	0.0043	0.0020
34	0.0317	0.0023	0.0000	0.0293	0.0417	0.0021	0.0919	0.0731	0.0012	0.0175	0.0020	0.0000

Table A1b. Small (0.5km radius) landscape scale coverages as fractions of total area

site	hemlk	iceplnt	indust	manz	maple	marsh	oakcomp	oak	oakbay	oakconfr	oakgrass	ocean
1	0.0000	0.0000	0.0146	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2532	0.1281	0.0000	0.1251	0.0000	0.0000
3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1122	0.1122	0.0000	0.0000	0.0000	0.0000
4	0.0012	0.0000	0.1773	0.0000	0.0030	0.0000	0.0916	0.0710	0.0139	0.0068	0.0000	0.0000
5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0579	0.0417	0.0000	0.0162	0.0000	0.0000
6	0.0000	0.0000	0.0000	0.0000	0.0028	0.0000	0.1934	0.1934	0.0000	0.0000	0.0000	0.0000
7	0.0331	0.0000	0.0195	0.0000	0.0000	0.0017	0.0148	0.0148	0.0000	0.0000	0.0000	0.0000
8	0.0000	0.0000	0.0000	0.0000	0.0000	0.1232	0.0166	0.0166	0.0000	0.0000	0.0000	0.0000
9	0.0000	0.1119	0.0000	0.0000	0.0000	0.0064	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
10	0.0007	0.0000	0.1341	0.0000	0.0000	0.0062	0.0004	0.0004	0.0000	0.0000	0.0000	0.0000
11	0.0051	0.0000	0.0000	0.0000	0.0000	0.0031	0.0805	0.0805	0.0000	0.0000	0.0000	0.0000
12	0.0011	0.0000	0.1296	0.0000	0.0000	0.0000	0.0082	0.0082	0.0000	0.0000	0.0000	0.0000
13	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1560	0.1560	0.0000	0.0000	0.0000	0.0000
14	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002	0.0002	0.0000	0.0000	0.0000	0.0000
15	0.0000	0.0000	0.0224	0.0000	0.0228	0.0209	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
16	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
17	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
18	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
19	0.0000	0.0000	0.0215	0.0000	0.0000	0.0123	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
20	0.0000	0.0000	0.0177	0.0000	0.0000	0.0163	0.0043	0.0043	0.0000	0.0000	0.0000	0.0000
21	0.0000	0.0000	0.0000	0.0000	0.0340	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
22	0.0000	0.0000	0.0000	0.0000	0.0000	0.0446	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
23	0.0007	0.0000	0.0067	0.0000	0.0037	0.0000	0.1906	0.1056	0.0337	0.0513	0.0000	0.0000
24	0.0000	0.0000	0.2205	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
25	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0068	0.0068	0.0000	0.0000	0.0000	0.0000
26	0.0000	0.0000	0.0212	0.0000	0.0000	0.0000	0.0862	0.0862	0.0000	0.0000	0.0000	0.0000
27	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1294	0.1253	0.0000	0.0040	0.0000	0.0000
28	0.0000	0.0000	0.0000	0.0000	0.0000	0.0555	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
29	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0597	0.0327	0.0000	0.0270	0.0000	0.0000
30	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0240	0.0240	0.0000	0.0000	0.0000	0.0000
31	0.0652	0.0033	0.0121	0.0000	0.0000	0.0202	0.0665	0.0623	0.0000	0.0043	0.0000	0.0000
32	0.0239	0.0000	0.0000	0.0000	0.0000	0.0000	0.0197	0.0105	0.0092	0.0000	0.0000	0.0000
33	0.0000	0.0000	0.0225	0.0000	0.0000	0.0000	0.0036	0.0036	0.0000	0.0000	0.0000	0.0000
34	0.0165	0.0026	0.0027	0.0000	0.0000	0.0000	0.0480	0.0435	0.0000	0.0000	0.0045	0.0000

Table A1b. Small (0.5km radius) landscape scale coverages as fractions of total area

site	park	pavedroad	prncrp	poisnoak	railline	resid	rural	sagecomp	sage	sagehemcoy	tanoak	willow
1	0.0000	0.0014	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0022
2	0.0082	0.0164	0.0095	0.0015	0.0000	0.0484	0.0446	0.0000	0.0000	0.0000	0.0000	0.0521
3	0.0000	0.0235	0.0249	0.0000	0.0000	0.0165	0.0540	0.0000	0.0000	0.0000	0.0000	0.0549
4	0.0000	0.0144	0.0012	0.0000	0.0000	0.0813	0.0064	0.0000	0.0000	0.0000	0.0000	0.0349
5	0.0000	0.0337	0.0041	0.0000	0.0000	0.2191	0.0318	0.0725	0.0725	0.0000	0.0000	0.0616
6	0.2390	0.0021	0.0000	0.0000	0.0000	0.0183	0.0000	0.0000	0.0000	0.0000	0.0000	0.0261
7	0.0000	0.0213	0.0000	0.0011	0.0076	0.0600	0.0000	0.0374	0.0087	0.0286	0.0000	0.0480
8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0335	0.0000	0.0000	0.0000	0.0000	0.1376
9	0.0000	0.1159	0.0000	0.0000	0.0000	0.0061	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
10	0.0013	0.0397	0.0011	0.0084	0.0562	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1049
11	0.0000	0.0091	0.0203	0.0000	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000	0.0000	0.0357
12	0.0000	0.0129	0.0329	0.0046	0.0000	0.0563	0.0000	0.0000	0.0000	0.0000	0.0014	0.0549
13	0.0000	0.0150	0.0000	0.0000	0.0000	0.3082	0.0000	0.0000	0.0000	0.0000	0.0000	0.0713
14	0.0000	0.0000	0.0045	0.0000	0.0000	0.0027	0.0338	0.0000	0.0000	0.0000	0.0000	0.0000
15	0.0000	0.0077	0.1727	0.0000	0.0000	0.0119	0.0215	0.0000	0.0000	0.0000	0.0000	0.0798
16	0.0000	0.0235	0.0000	0.0000	0.0000	0.0000	0.0123	0.0000	0.0000	0.0000	0.0000	0.0000
17	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0476
18	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0138
19	0.0000	0.0099	0.3234	0.0000	0.0000	0.0085	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003
20	0.0000	0.0083	0.0158	0.0000	0.0000	0.0002	0.0091	0.0000	0.0000	0.0000	0.0000	0.0000
21	0.0000	0.0000	0.0193	0.0000	0.0000	0.0000	0.0198	0.0000	0.0000	0.0000	0.0000	0.0049
22	0.0000	0.0000	0.0000	0.0000	0.0000	0.0061	0.0203	0.0000	0.0000	0.0000	0.0000	0.0968
23	0.0000	0.0192	0.0217	0.0000	0.0000	0.2454	0.0208	0.0000	0.0000	0.0000	0.0000	0.0187
24	0.0000	0.0341	0.0000	0.0000	0.0000	0.0329	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
25	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0039
26	0.0000	0.0245	0.0040	0.0000	0.0000	0.3559	0.0037	0.0238	0.0238	0.0000	0.0000	0.0490
27	0.0000	0.0173	0.0000	0.0000	0.0000	0.4032	0.0715	0.0000	0.0000	0.0000	0.0000	0.0882
28	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0487
29	0.0000	0.0000	0.0593	0.0000	0.0000	0.0000	0.0327	0.0000	0.0000	0.0000	0.0000	0.0000
30	0.0000	0.0206	0.0000	0.0000	0.0000	0.0000	0.0000	0.0015	0.0000	0.0015	0.0000	0.0000
31	0.0000	0.0235	0.0000	0.0007	0.0062	0.0000	0.0059	0.0265	0.0265	0.0000	0.0000	0.0353
32	0.0000	0.0046	0.0000	0.0000	0.0001	0.0000	0.0130	0.2103	0.0000	0.2103	0.0000	0.0127
33	0.0000	0.0394	0.0127	0.0000	0.0000	0.1699	0.0000	0.0000	0.0000	0.0000	0.0000	0.0078
34	0.0372	0.0253	0.0000	0.0041	0.0006	0.1748	0.0000	0.0000	0.0000	0.0000	0.0000	0.0184

Table A1b. Small (0.5km radius) landscape

site	veg	numveg	pernveg	annveg
1	0.0104	3	0.0059	0.9777
2	0.7679	8	0.4330	0.3150
3	0.4277	5	0.3016	0.5244
4	0.4754	10	0.2935	0.2055
5	0.2970	9	0.2269	0.4027
6	0.6300	7	0.5588	0.1615
7	0.6027	14	0.2077	0.6689
8	0.5152	6	0.1565	0.7460
9	0.0306	5	0.0077	0.6265
10	0.4427	8	0.1746	0.4515
11	0.7564	8	0.4194	0.5655
12	0.3791	7	0.1020	0.6604
13	0.6424	5	0.2351	0.3745
14	0.8945	3	0.7032	0.2552
15	0.3216	4	0.2753	0.5437
16	0.1208	2	0.0031	0.9610
17	0.0651	3	0.0496	0.9389
18	0.0173	2	0.0138	0.9862
19	0.0536	2	0.3597	0.6128
20	0.1528	3	0.0227	0.9414
21	0.8333	6	0.8396	0.1291
22	0.8364	6	0.6758	0.2727
23	0.5901	10	0.5330	0.1429
24	0.0652	1	0.0000	0.6962
25	0.2550	4	0.0158	0.9806
26	0.4785	8	0.3159	0.2485
27	0.3890	9	0.2993	0.1649
28	0.1224	5	0.0562	0.8652
29	0.4961	4	0.1827	0.7706
30	0.1078	4	0.0386	0.9401
31	0.7296	12	0.3292	0.5753
32	0.8655	8	0.3903	0.5886
33	0.6722	7	0.0672	0.6529
34	0.2784	11	0.1283	0.5523

APPENDIX 2

SUBFAMILY MORPHOSPECIES NOTES FOR ICHNEUMONIDAE

The following notes were used to build a reference collection for all ichneumonid morphospecies collected using Malaise traps or reared from sentinel *Trichoplusia ni* larvae.

Within each subfamily section, each morphospecies is named by the first three letters of the subfamily plus an identifying number. Morphospeices that were later split off from an existing group were named with additional letter.

Reference collection specimens are listed at the end of each description, following a hash tag (#); this collection is located in the UCSC Natural History Museum, with the exception of specimens sent to Dr. Robert Kula, USDA Systematic Entomology Lab/Smithsonian Institution, for identification.

Anomaloninae

Only one morph, which was never collected in Malaise trap samples, only reared from sentinel *T ni*.

Banchinae

BAN1: small-med insect. Black&red body: red notalus, abd blk wi/red stripe pattern. v long, curved ovipositor. Yellow legs. White mandibles, face otherwise all black #s 654.

BAN2: med insect. Like BAN1 but mandibles dark and legs brn & face wi/lines between eyes. Body blk and brn. Scutell & mesopleuron brn. Aereolet sessile and closed (but closing vein is spectral). Abd blk. V. long, curved ovipositor. #s 325, 503, 1424.

BAN2A: similar to BAN2, but body all blk except for stripes on abd. Aereolet open. 2m-cu has 2 bullae. Ovip sheath long and curled. Ovip med-long and curled ventrally. # 577, 578, 579, 580, 1343.

BAN3: med insect. Body blk and red (notalus). Scutell & mesopleuron brn. No aereloet. Abd blk wi/lots of orange and sculpted. T3 and tarsi have blk/wht banding pattern. V. long, curved ovipositor and ovip. sheath is long, curled. Black face #s 130.

BAN4: med insect. body all blk, abd sculpturing. Legs red. v long, curved ovipositor, with curly sheath. #s 1343.

BAN5: med insect. Blk body, but brn patterning on abd. yel legs. v long, straight ovipositor wi/curly sheath. #s 1188, 1344.

BAN6: small-med insect. yel/blk thorax, blk patterned abd. short, straight ovipositor. T3=blk/wh/blk. #s 1393.

BAN7: v different abd shape (stiff), but same brn/blk thorax coloration as BAN1, etc. T3 = brn.
v short ovipositor. #s 322, 342, 764, 1259, 1295.

BAN8: small insect. Abd & legs all red. Thorax red & blk. Blk head wi/markings near eyes. Odd aereolet shape. Antennae have transparent patch. #s 1425, 1427.

Campopleginae

Primary distinguishing characters:

1. Forewing aereolet –petiolate vs. sessile & open vs. closed. Most genera have closed aereolets.
2. Abdominal color.
3. Hind tibia –color/pattern.

CAM1: Red abd. aereolet petiolate and closed. Femurs = white base, red rest. T3 = red/wh/red.
#s 117, 164, 123, 333, 387, 420, 421.

CAM1A: same as CAM1 but T3 = red. #s 1080.

CAM2: aereolet petiolate and closed. Black abdomen with red, petiole blk. Femurs = yellow. T3 = brn/wh/brn or brn/yel/brn #s 108, 157, 196, 198, 199, 200, 201, 202, 218, 219, 121, 122, 126, 148, 150, 332, 252, 275, 300, 264, 265, 281, 298, 301, 332, 388, 610, 657, 720, 984, 1085, 1086, 1129, 1287, 1338, 1342.
(Destroyed specimen: 282).

CAM2A: Similar to CAM2, but yellowish color to wings and abdomen is entirely black (lacks red patterning). T3 = blk/wh/blk. Short ovip. #s 543, 644, 645, 652, 655, 766, 771, 1110.
(Destroyed specimens: 323, 422, 423, 648, 651, 768, 770)

CAM3: Like 2A but T3 = red and ovip = med length. aereolet petiolate & closed. Blk abdomen. Femur = red. #s 242, 326, 418, 390, 425, 334, 640, 641, 1093.
(Destroyed specimens: 245, 248, 243, 424, 504)

CAM4: aereolet petiolate and closed, but faint. Abdomen black with red pattern. Femur and T3 = red. #s 101, 194, 195, 197, 605, 606, 609, 643, 646, 649, 669, 767.

CAM5: aerelolet sessile and closed. Body is black, petiole blk but some red patterning on abdomen. T3 = brn/wh/brn. T1 & T2 = yel & wh stripes. #s 118, 187, 299, 359, 400, 427, 627, 628, 950, 1289, 1410, 1411.

CAM6: aereolet sessile and open. Black abdomen, blk petiole. T3= blk/wh/blk, pattern continues down tarsi. #s 249, 544, 616, 617, 1246.

CAM6A: Similar to CAM6, but aereolet even more widely open, T3 = brn/yel/brn (more subtle banding). Short Ovip and ovip sheath. #s 314, 426, 615, 618, 656, 1316.

CAB6B: like CAM6 but legs blk, T3 has dark base & rest mostly white. # 1421.

CAM7: aereolet petiolate (shorter than 1-3?) and closed. Abd blk with same red patterning as earlier CAMs, petiole black. Black legs, tibia has white base. Mandible is black instead of pale. #s 313.

CAM8: aereolet petiolate & closed (& v. small, on diagonal). Abd petiolate and clubbed shape wi/2nd segment elongated. T3 = br/wh/br but not v dark. Mandible is pale. v. long ovipositor. #520.

CAM9: large. Aereolet sessile & closed. Abd blk & red. T3 =dark. # 1435.

CAM10: aereolet wide open. Abd red and blk, thorax has red. face = pale. ovip = long, T3= brown. # 1436.

Cremastinae

CRE1: med-small insect. Black thorax. Red abdomen and legs. Pretty face markings. #s 181.

CRE2: small insect. Black body. Light brown legs. Stigma shape is deep. Ovipositor longer than abd. white face. #s 283.

CRE3: like CRE2 but darker legs and dark face. Stigma has shallow shape. #s 802.

Ctenopelmatinae

CTE1: #s 207.

Diplazontinae

DIP1: Large red band across abdomen. No aereolet. T3 = black/white/black/yellow. Abdomen has blk petiole segment, face wi/2 vertical white bands near eye. #s 475, 545, 670, 671, 1194, 1390.

DIP1A: Like DIP1 but red abd has red petiole seg, black tip. T3 = bl/wh/bl/yel. Face wi/vertical bands medial to eyes. #s 168, 384, 429, 1195, 1197.

DIP1B: like DIP1 but abd entirely black. T3= blk/wh/bl/yel; face with vert lines medial to eyes. #s 1423.

DIP2: Large red band across abdomen. No aereolet. T3 = all brown/yellow. Face with white star. #s 119, 154, 176, 189, 276, 304, 305, 306, 316, 337, 340, 357, 383, 393, 394, 431, 469,526, 527, 532, 534, 676, 677, 801, 910, 973, 1171.

DIP2A: Similar to DIP2, but lack of red band on abdomen, more brown striation pattern, blk petiole. Laterally flattened abd. No aereolet. Thoracic light patch may also be smaller. Face wi/ white star. T3 = yellow #s. 233, 339, 355, 356, 358, 391, 474, 476, 477, 478, 479, 550, 687, 765, 1367.

DIP2B: Similar to DIP2A but dorso-ventrally flattened abd. Blk/brwn striation pattern abd. No aereolet. Grey face. T3 = yellow. #s 672, 760, 1063, 1065, 1422.

DIP2C: Like DIP2B but yellow face (distinctive). Abd rounded, not flattened. #s 376, 392, 472, 803, 804, 805, 806, 1220, 1263.

DIP3: Abd all blk, incl petiole. T3 banded ½ to 2/3 white/ ½ to 1/3 blk. Aereolet closed. Face has small star. #s 600, 601, 977, 978, 1091, 1050.

DIP4: Stouter insect. No aereolet. Abdomen is all black & shorter. T3 = white base; rest is brown/black. Wht star on face. #s 128, 165, 341, 812, 813, 1153, 1346.

DIP4A: Similar to DIP4, but abdomen longer. T3 all dark. No star face. Red legs. #s 1049.

DIP4B: Like DIP4A but thoracic patch is minimal. #s 1089.

DIP5: Abdomen is red/brown, but with mostly black petiole segment & black at the abd. tip. Aereolet closed, briefly petiolate (but faint). T3 = all reddish brown. Face with white star AND lines medial to both eyes. #s 129, 336, 385, 428, 846.

DIP6: White face, all coxae white as is most of thorax ventral side. Dorsal side blk, petiole blk. Aereolet open. T3 white to blk gradation, F3 brown. #430.

DIP7: med insect, larger than all other DIPs. body all blk, underside of abd is not concave like all other DIPs. Legs red except T3 wh base, rest blk. v long C3. Face has white star. #s 1046.

Ichneumoninae

ICH1: large bodied. Blue-black shimmery body. #s 120, 415, 564, 563, 565 (with 563 and 565 being more metallic than the rest).

ICH2: large bodied. Yellow & black waspy patterned body. #s 288.

ICH2A: similar to 2, but more or/br color than yellow. #753 (see also specimen from September 2005 sentinel looper). 2 & 2A have the same L3 banding pattern, and both are male.

ICH2B: Similar to 2 and 2A, but legs all red. C3 is mixed red/blk. No stripes on abd, all red. #s 1431.

ICH3: large bodied. Reddish-brown & stout body. Head = red. Dark colored ocelli & dark stripe across middle of abdomen. #s 583.

ICH3A: similar to ICH3 but light colored ocelli, and diff abd patter. #s 290.

ICH4: all brown (no blk head) narrowish abdomen. #586, 587, 588, 589, 604, 590.

ICH5: pale red/yel, dark antennae are straightish OR thick and curly, yellow face (m) OR face same red color as body (f) but dark oceli, no leg banding. #s 239, 584.

ICH6: v. much like ICH4, all blk, but lighter, not curled antennae. Light patches (thyridia) present on 2nd metasomal segment. #s 557.

ICH7: blk body, legs brn. curled, thicker antennae bent up. Shorter ovipositor (1/2 as long as PIM1). #s 293.

Labeninae

LAB1: #s 167.

LAB2: #s 1045.

Mesochorinae

MES1: small bodied. Light brown. #238.

MES2: v. small bodied. Red/brn pattern. #s 329, 375, 417, 1290.

Metopiinae

MET1: Small, black-bodied w/brown legs. Aereolet wide open, sessile. Fuzzy, whiteish face. Dark antennae. 1st pair of legs tucked up. F3 = dark brn, C3 = blk. Short ovip. #s 174, 213, 266, 327, 515.

MET2: smaller than MET1, black body, yel-brown legs. Coxae all yel/brn. Aereolet closed but vein faint. V. short ovip. Brown, hairy face. Red/brn antennae. #s 209.

MET2A: like MET2, blk body, brn/yel legs BUT C1&2 are pale, C3 darker/brn, brn face & red/brn antennae, but aereolet clearly closed & sessile. #542, 1294.

MET3: larger than MET1. Blk face, no marks (m) OR light mark on face ventral to antennae (f). Shape of hind femur. F3 = red-brn, C3 = red-brn. #s 160, 210, 319, 594, 595, 596, 597, 1092.

Orthocentrinae

Primary distinguishing characters:

1. Abdomen color
2. Face color (white vs. blk/brn) is a sexually dimorphic trait in this subfamily, and specified below.
3. Forewing aereolet open/closed (always sessile)
4. Leg color

ORT1: small-medium insect. Black body & petiole, w/red thoracic markings. Legs = brn, Face = brn. Aereolet sessile & closed, v. short ovip. dark stigma. #s 173.

ORT2: small insect. Black body, blk petiole, abd striation pattern. White face (m), OR brown face (f). Legs: pairs 1 & 2= white, 3 = brown & white. Aereolet sessile & closed. Dark stigma. Straight, stiff abd shape. Antennae curled back. #s 112, 221, 222, 223, 228, 900, 907, 912.

ORT3: “morph C” v. small insect. Black body. Brown legs. Blk/brn face (f) OR white face (m). Aereolet open. Abdomen often squashed & ovipositor comes out linear or at 90° angle; stiff shape. “Horsehead” cell is more of a giraffe head. Pale stigma. No different types A-C. #s 105, 110, 131, 132, 143, 182, 183, 192, 193, 211, 229, 234, 268, 269, 296, 297, 349, 351, 352, 353, 360, 361, 362, 402, 403, 448, 457, 460, 514, 754, 755.

ORT4: V. small, brown-black insect. Aereolet sessile and open (faint vein). Long, straight ovipositor sheath, ovip med & straight. Curled antennae. Abd not as linear as other ORTS. #s 308, 310, 364, 365, 366, 369, 370, 371, 372, 373, 412, 513, 516, 591, 592, 593.

ORT5: small insect. Body all blk, but legs are wht/yellows (prs 1 &2) or (pr 3) have F3 = yellow & T3 = blk./wht/blk banding which continutes down tarsi. Leg coloration is different from ORT2. #s 312, 1116.

Phygadeuontinae (now called Cryptinae)

keyed using *Hymenoptera of the World*, hence the older subfamily name and mspp codes.

Primary distinguishing characters:

1. Body size
2. Abdomen color
3. Ovipositor length
4. Forewing (“lat”) vein: aereolet-wing margin
5. Antennal color
6. Coxal color
7. Propodeum length/shape

PHY1: Small insect. Abd red, but blk pet & tip. Short ovip. Lat vein is long. #s 151, 161, 163, 206, 215, 262, 317, 318, 324, 344, 347, 348, 350, 363, 379, 398, 440, 441, 444, 521, 523, 525, 556, 558, 559, 679, 686, 689, 694, 703, 712, 714, 721, 737, 738, 739, 817, 818, 821, 824, 826, 832, 848, 853, 874, 875, 901, 951, 961, 962, 974, 976, 989, 991, 1007, 1040, 1041, 1046, 1073, 1075, 1098, 1119, 1135, 1137, 1242, 1247, 1264, 1318, 1319, 1321, 1322, 1323, 1372, 1375, 1376, 1381, 1382, 1407.

PHY1A: Small insect. abd red, but blk tip only. Short ovip. #s 169, 346, 711, 736.

PHY1B: Small insect. Abd all red, incl petiole. Ovip short. #s 691, 816, 1048, 1049, 1072.

PHY2: Small insect. Abd red, but brn pet & blk tip. Med ovip. #s 113, 315, 522, 850.

PHY3: Small insect. Abd red but darker pet & blk tip. Med-long ovip. #s. 175.

PHY4: Small insect. Abd red, but blk pet segment. v black antennae. short ovip. Lat vein short #s 159, 259, 260, 287, 681, 682, 701, 1239, 1320.

PHY5: Small insect. Brown body, but reddish thoracic markings just above C1. #s 258, 263, 702, 1118, 1238, 1369.

PHY6: Small insect. Abd blk wi/red only marking segment divisions. Legs red. Short, straight ovip. Lat vein extends to wing margin. #s 561, 990, 914, 1036, 1181, 1384.

PHY6A: Like PHY6, but abd shape is much narrower. Short ovip. Lat vein is short. Tightly curled ant. #s 186, 257, 261, 320, 443, 467, 717, 718, 735, 779, 975.

PHY6B: Like PHY6 but abd is entirely black (no red at all) & med ovip. #s 188.

PHY7: Small insect. Abd blk wi/red splotch pattern. Dark/brn legs. Lat vein short. Thick, curled antennae. #s 524, 680, 685, 908, 911.

PHY8: smaller bodied. All black, “disc” shape. Thick, black, curly antennae. #s 277, 1038.

PHY8A: small insect. blk body, but abd is reddish-black. Thick, curly antennae. Short ovip. Dark coxae, Lat vein not complete but longish, black antennae. #s 988, 1324, 1369, 1374.

PHY8B: Like PHY8A but v. pale C1&2, Lat vein is short, antennae brownish esp. at base. #s 927, 958, 1008, 1035, 1293.

PHY8C: Like PHY8A but coxae more uniformly colored, more red than yellow. Red antennae. Lat vein is complete to wing margin. #s 562, 833, 1138.

PHY8D: Like PHY8C but antennae are dark. Coxae yellow, abd dark, lat vein complete. #s 397, 742.

PHY9: small insect. blk thorax, red abd, but blk petiole & tip. Red/pale antennae. #s 273, 345, 468, 555, 759, 780, 782, 783, 784, 814.

PHY9A: like PHY9 but petiole segm red & thorax has reddish markings above C2&3. #s 722, 781.

PHY10: All red abd incl pet & tip. Thorax entirely blk. all black face or may have faint white marks between eyes. Red legs. #s 251, 451, 582, 783.

PHY11: v. small insect. Blk body. C1&2 pale, yel legs, antennae dark. Lat vein (faintly) complete. #s 172, 177, 207, 212, 214, 272, 286, 407, 408, 414, 446, 517, 683, 684, 695, 715, 740, 829, 834, 1078, 1120, 1184, 1325, 1373.

PHY11A: Like PHY11 but all coxae are black, instead of pale/white. Antennae black. Lat vein complete. #s 267, 271, 311, 377, 378, 380, 409, 411, 445, 704, 831.

PHY12: small insect. All blk, but yellow/brn legs & color splotch on abd (otherwise like PHY11) Lat vein complete. coxae are all brown. Dark antennae #s 270, 382, 1098, 1371, 1373.

PHY12A: like PHY12 but antennae pale brn. Lat vein complete. Coxae uniform dark color. #s 1183.

PHY12B: like PHY12 but Lat vein short. Coxae all dark brn, antennae dark #s1026, 1031, 1095, 1097.

PHY13: v small insect. body all blk except abd has blk petiole, rest brn wi/yellow stripe. C1&2are white, C3 is dark/brn, legs are brn. Antennae have pale scape. #s 285, 1074, 1418.

PHY14: small insect. Blk head & thorax. narrow, elongate Abd wi/ blk petiole blends to yellow patchy, then brn tip. Legs = yellow. Antennae have dark scape. #s 166.

PHY15: v. small insect. blk thorax. Yel/brn abd. yel legs. #s 114, 153, 278, 280, 309, 410, 447, 454, 465, 505, 688, 741, 815, 928, 1076, 1133, 1185, 1245, 1265, 1379, 1380, 1420.

PHY15A: v small insect. blk thorax but brn notalus. aereolet open but regular-5sided shape. yel/brn abd. short ovip. #s 367, 1249.

PHY16: v small insect. blk thorax, brn notalus like PHY15A, but irregular-shaped aereolet. #s 235.

PHY17: med-sized insect. Red abd. med-length, straight ovip. Curly ovip sheath.#s 179, 205220.

PHY18: med-sized insect. Red abd wi/black tip. Med-length ovip. Curly ovip sheath. #s 124.

PHY19: med-small insect. Red abd, but blk pet & tip. Pet is round, but abd shape is elongate Legs: blk troch and coxae, red F & T, blk tarsi. #s 331.

PHY20: medium-small bodied. “fairy” shape. Body all red, except black head (wi/red face), abd extends linearly back from the thorax. v short ovip. fairly ridgy propodeum. #s 452, 1429.

PHY21: med-small insect. similar to PHY20, also “fairy” shape, BUT all red/brn incl head (but dark eyes). Short ovip wi/curly sheath, but longer than PHY20 ovip. Propodeum less ridgy than PHY20. #s 1044.

PHY22: “little brown guy” with dark head. Long ovipositor. Extended ridges on back of propodeum/little ridges. #s 1047, 1386.

PHY23: small insect. blk thorax. Brn abd, but blk petiole. med ovipositor (sometimes straight, sometimes gentrly curved). Red legs. #s 104, 254, 256, 274, 321, 343, 368, 381, 551, 553, 692, 693, 697, 698, 699, 700, 855, 858, 902, 905, 913, 1020, 1039, 1094, 1096, 1099, 1180, 1240, 1377, 1378, 1419.

Pimplinae

PIM1: blk body, legs brn. medium ovipositor. 4-sided aereolet, closed, sessile. #s 145, 180, 217, 240, 250, 281, 289, 292, 386, 461, 500, 501, 502, 581, 1291.

PIM2: blk body, legs brn. very diff. abdominal shape from other PIMs. Aereolet 4-sided and sessile. Curly, bristly ovipositor sheath. Med ovipositor. #s 237.

PIM3: Same as PIM1 but T3 & tarsi have bl/wh/bl/etc. pattern. Med ovipost. #653.

PIM3A: Like PIM3 but abd has red pattern wi/blk (not all blk). #s 1428.

PIM4: Black. T3 faint blk/wh/blk pattern. Aereolet closed, sessile, 4-sided. Ovip med-long, long curly ovip sheath. # 576.

Tersilochinae

TER1: #s 828.

Tryphoninae (Have pectinate tarsi & smooth side to thorax)

TRY1: largest bodied. Brown. #s. 330, 416, 1009, 1043.

TRY2: Can see the stalked egg cluster gathered near the ovipositor. #s 463.

Xoridinae

XOR1: #s 170.

APPENDIX 3

TRICHOPLUSIA NI COLONY ESTABLISHMENT AND ALTERNATIVE SENTINEL METHODS USED IN 2005 AND 2006.

Colony establishment

In 2005, we created and maintained a *T. ni* colony in a greenhouse at UCSC, using individuals collected on local farms—caterpillars collected for this purpose had a parasitism level of 28% by parasitic wasps and flies combined. From this colony, we used second to third instar larvae for use in field experiments at low numbers (three loopers per plant, eight plants per farm). In 2006 and 2007, a permit from APHIS allowed us to adjust the experimental methods to use younger (mostly first instar) larvae purchased in large quantities from Bio-Serv. This change was a significant methodological improvement because younger instar larvae are primarily attacked by hymenopteran parasitoids whereas older larvae are predominantly attacked by dipteran (Tachinidae) parasitoids.

Egg attachment

In 2005, we placed 2nd to 3rd instar larvae onto collard plants at each site. In 2006, we attached 1cm x 1cm egg sheets pinned onto collard leaves the evening before field exposure.

Looper containment apparatus

In 2005, larvae were exposed in the field for only five days, and at 33 sites. In 2006, the methods were the same as for 2007 except that all 33 sites were included. Fewer sites were included in 2007 due to farm closures and management changes. The landscape characterization methods were conducted for all 33 sites included in the multiple years of this study, not just for the 28 sites used for the 2007 sentinel pest study. Only 2007 experiments yielded sufficient parasitism outcomes to conduct data analysis.

Rationale for adapting these methods between years

The experiments in 2005 and 2006 did not yield sufficient data for analysis. In 2005, advanced larval development stages (2nd instar and above) precluded attack by the majority ichneumonid wasps (only one individual), but facilitated attack by tachinid flies. In 2006, after switching to the eggsheet attachment method which allowed for exposure of earlier instar larvae in the field, local lepidopteran and parasitic hymenoptera population sizes seemed to be smaller than in the previous two years (based on my malaise trap captures as well as personal communications with growers and Jan Washburn), and very low measured rates of parasitism on the sentinel loopers at two, zero, and six sites in May, June, and August, respectively—detecting no parasitism on sentinels at the remaining sites. This younger larvae approach was more successful in 2007, however.

BIBLIOGRAPHY

Aguilar-Amuchastegui, N., and G. M. Henebry. 2007. Assessing sustainability indicators for tropical forests: Spatio-temporal heterogeneity, logging intensity, and dung beetle communities. Forest Ecology and Management **253**:56-67.

Altieri, M. A., and D. K. Letourneau. 1982. Vegetation managment and biological control in agroecosystems. Crop Protection **1**:405-430.

Araj, S., S. Wratten, A. Lister, and H. Buckley. 2008. Floral diversity, parasitoids and hyperparasitoids--A laboratory approach. Basic and Applied Ecology **9**:588-597.

AWQA. 2008. Agriculture Water Quality Alliance http://www.awqa.org.

Baggen, L. R., and G. M. Gurr. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Biological Contol **11**:9-17.

Baldi, A. 2003. Using higher taxa as surrogates of species richness: A study based on 3700 Coleooptera, Diptera, and Acari species in Central-Hungarian reserves. Basic and Applied Ecology **4**:589-593.

Balvanera, P., G. C. Daily, P. R. Ehrlich, T. H. Ricketts, S.-A. Bailey, S. Kark, C. Kremen, and H. Pereira. 2001. Conserving Biodiversity and Ecosystem Services. Science **291**:2047.

Barbosa, P. 1998. Conservation Biological Control. Academic Press, San Diego.

Batary, P., A. Baldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B **278**:1894-1902.

Beal, D. J. 2005. SAS code to select the best multiple linear regression model for multivariate data using information criteria. Science Applications International Corporation, Oak Ridge, TN.

Beane, K. A., and R. L. Bugg. 1998. Natural and artificial shelter to enhance arthropod biological control agents. Pages 239-253 *in* R. Bugg, editor.

Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, CA.

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. Science **325**:1121-1124.

Bennett, A. B., and C. Gratton. 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. Landscape and Urban Planning **104**:26-33.

Beretti, M., and D. Stuart. 2008. Food safety and environmental quality impose conflicting demands on Central Coast growers. California Agriculture **62**.

Bianchi, F., P. Goedhart, and J. Baveco. 2008. Enhanced pest control in cabbage crops near forest in the Netherlands. Landscape Ecology **23**:595-602.

Bianchi, F., W. van Wingerdern, A. Griffoen, M. van der Veen, M. van der Straten, R. Wegman, and H. Meeuwsen. 2005. Landscape factors affecting control of *Mamestra brassicae* by natural enemies in Brussels sprout. Agriculture Ecosystems & Environment **107**:145-150.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B **273**:1715-1727.

CAFF. 2006. Farmscaping for conservation and on-farm benefits. Community Alliance with Family Famers www.caff.org/.

CAFF. 2010. Hedgerows, CAFF Farmscaping Program. California Alliance with Family Farmers http://caff.org/programs/bio-ag/hedgerows/.

Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters **6**:857-865.

CCOF. 2008. Statistics by chapter 2004-2007. California Certified Organic Farmers http://www.ccof.org/pdf/CCOFStatistics08.pdf.

Chan, K. M. A., M. R. Shaw, D. R. Cameron, E. C. Underwood, and G. C. Daily. 2006. Conservation planning for ecosystem services. PLoS Biology **4**:2138-2152.

Chang, G. C. 1996. Comparison of single versus multiple species of generalist predators for biological control. Environmental Entomology **25**:207-212.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters **14**:922-932.

Clarke, K. R., and R. M. Warwick. 1994. Linking Community Analysis to Environmental Variables. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth, England.

Corbett, A., and J. A. Rosenheim. 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landsdcape. Ecological Entomology **21**:155-164.

da Silva, P. M., C. A. S. Aguiar, J. Niemela, J. P. Sousa, and A. R. M. Serrano. 2008. Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. Agriculture, Ecosystems, and Environment **124**:270-274.

Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators **1**:3-10.

Darling, D. C., and L. Packer. 1988. Effectiveness of Malaise traps in collecting Hymenoptera--The influence of trap design, mesh size, and location. Canadian Entomologist **120**:787-796.

Davidson, J., and H. G. Andrewartha. 1948. The influence of rainfall, evaporation, and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). The Journal of Animal Ecology **17**:200-222.

Deans, A. M., S. M. Smith, J. R. Malcolm, W. J. Crins, and M. I. Bellocq. 2007. Hoverfly (Syrphidae) communities respond to varying structural retention after harvesting in Canadian peatland black spruce forests. Environmental Entomology **36**:308-318.

DeBach, P., and D. Rosen. 1991. Biological Control by Natural Enemies. Cambridge University Press, New York.

Devotto, L., C. delValle, R. Ceballos, and M. Gerding. 2010. Biology of *Mastrus ridibundusi* (Gravenhorst), a potential biological contorl agent for area-wide management of *Cydia pomonella* (Linneaus) (Lepidoptera: Tortricidae). Journal of Applied Entomology **134**:243-250.

Divan, A. M., P. L. de Oliveira, C. T. Perry, V. L. Atz, L. N. Azzarini-Rostirola, and M. T. Raya-Rodriguez. 2009. Using wild plant species as indicators for the accumulation of emissions from a thermal power plant, Candiota, South Brazil. Ecological Indicators **9**:1156-1162.

Earnshaw, S. 2004. Hedgerows for California agriculture. Community Alliance with Family Farmers, Davis, California.

Ehler, L. E., and J. C. Miller. 1978. Biological control in temporary agroecosystems. Entomophaga **3**:207-212.

Eliopoulos, P. A., and G. J. Stathas. 2005. Effects of temperature, host instar, and adult feeding on progeny production by the endoparasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae). Environmental Entomology **34**:14-21.

Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecology Letters **8**:1299-1306.

Flint, M. L. 1990. Pests of the Garden and Small Farm. Univeristy of California Press, Oakland.

Flint, M. L., and S. H. Dreistadt. 1998. Natural Enemies Handbook. University of California Press, Oakland.

Frank, S. D., S. D. Wratten, H. S. Sandhu, and P. M. Shrewsbury. 2007. Video analyssi to determine how habitat strata affects predator diversity and predation of *Epiphyas postvittana* (Lepidoptera : Tortricidae) in a vineyard Biological Control **41**:230-236.

Fraser, S. E. M., C. Dytham, and P. J. Mayher. 2007. Determinants of parasitoid abundance and diversity in woodland habitats. Journal of Applied Ecology **44**:352-361.

Fraser, S. E. M., C. Dytham, and P. J. Mayhew. 2008. The effectiveness and optimal use of Malaise traps for monitoring parasitoid wasps. Insect Conservation and Diversity **1**:22-31.

Gaasch, C. M., J. Pickering, and C. T. Moore. 1998. Flight phenology of parasitic wasps (Hymenoptera: Ichneumonidae) in Georgia's Piedmont. Environmental Entomology **27**:606-614.

Geiger, F., J. Bengtsson, F. Berendse, W. W. Weisser, M. Emmerson, M. B. Morales, P. Ceryngier, J. Liira, T. Tscharntke, C. Winqvist, S. Eggers, R. Bommarco, T. Part, V. Bretagnolle, M. Plantegenest, L. W. Clement, C. Dennis, C. Palmer, J. J. Onate, I. Guerrero, V. Hawro, T. Aavik, C. Thies, A. Flohre, S. Hanke, C. Fischer, P. W. Goedhard, and P. Inchausti. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology **11**:97-105.

Gratton, C., and S. C. Welter. 1999. Does "enemy-free space" exist? Experimental host shifts of an herbivorous fly. Ecology **80**:773-785.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science **307**:550-555.

Herzog, D., and J. Funderburk. 1986. Ecological basis for habitat managment and pest control. Pages 217-250 *in* M. Kogan, editor. Ecological Theory and Integrated Pest Managment Practice. John Wiley & Sons, New York.

Hirst, A. J. 2008. Surrogate measures for assessing cyptic faunal biodiversity on macroalgal-dominated subtidal reefs. Biological Conservation **141**:211-220.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps, and their parasitoids? Journal of Animal Ecology **79**:491-500.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Stala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Hyatt, E. 2001. Editorial. Ecological Indicators **1**:1-2.

Idris, A. B., and E. Grafius. 1995. Wildflowers as nectar sources for Diadegma insulare (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). Environmental Entomology **24**:1726-1735.

Jervis, M. S., M. A. C. Kidd, M. D. Fitton, T. Huddleson, and H. A. Dawah. 1993. Flower visiting by hymenopteran parasitoids. Journal of Natural History **27**:67-105.

Jonsson, M., H. L. Buckley, B. S. Case, S. D. Wratten, R. J. Hale, and R. K. Didham. 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. Journal of Applied Ecology **49**:706-714.

Kido, H., D. L. Flaherty, C. E. Kennett, N. F. McCalley, and D. F. Bosch. 1981. Seeking the reasons for differences in orange tortrix infestations. California Agriculture **35**:27-28.

Kremen, C. 1994. Biological inventory using target taxa: A case study of the butterflies of Madagascar. Ecological Applications **4**:407-422.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: Their use in conservation planning. Conservation Biology **7**:796-808.

Kremen, C., N. M. Williams, and R. W. Thorp. 2007. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Science **99**:16812-16816.

Kreuss, A., and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. Oecologia **122**:129-137.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science **264**:1581-1584.

Landis, D. A., and F. D. Menalled. 1998. Ecological Considerations in the Conservation of Effective Parasitoid Communities in Agricultural Systems.*in* P. Barbosa, editor. Conservation Biological Control. Academic Press, San Diego.

Landis, D. A., F. D. Menalled, A. C. Costamagna, and T. K. Wilkinson. 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. Weed Science **53**:902-908.

Lavandero, B., S. Wratten, P. Shishehbor, and S. Worner. 2005. Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): Movement after use of nectar in the field. Biological Control **34**:152-158.

Lee, J. C., G. E. Heimpel, and G. L. Leibee. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parastioid wasp. Entomologia Experimentalis et Applicata **111**:189-199.

Letourneau, D. K. 1987. The enemies hypothesis: tritrophic interactions and vegetational diversity in tropical agroecosystems. Ecology **68**:1616-1622.

Letourneau, D. K., and M. A. Altieri. 1999. Chapter 14: Environmental Management to Enhance Biological Control in Agroecosystems. Pages 319-354 *in* T. Bellows and T. Fisher, editors. Handbook of Biological Control: Principals and Applications of Biological Control. Academic Press, San Diego.

Letourneau, D. K., I. Armbrecht, B. Salguero-Rivera, J. Montoya-Lerma, E. Jimenez-Carmona, M. C. Daza, S. Escobar, V. Galindo, C. Gutierrez, S. Lopez, J. Lopez-Mejia, A. M. Acosta-Rangel, J. Herrera-Rangel, L. Rivera, C. A. Saavedra, A. M. Torres, and A. Reyes-Trujillo. 2011. Does plant diversity benefit agroecosystems? A synthetic review. Ecological Applications **21**:9-21.

Letourneau, D. K., and B. Goldstein. 2001. Pest damage and arthropod community structure in organic vs. conventional tomato production in California. Journal of Applied Ecology **38**:557-570.

Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on teh suppression of arthropod herbivores in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics **40**:573-592.

Losey, J. E., and R. F. Denno. 1998. Positive predator-prey interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology **79**:2143-2152.

Lovell, S., M. Hamer, R. Slotow, and D. Herbert. 2007. Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. Biological Conservation **139**:113-125.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology **36**:533-536.

Mace, G. M., and J. E. M. Baillie. 2007. The 2010 biodiversity indicators: Challenges for science and policy. Conservation Biology **21**:1406-1413.

Maleque, M. A., H. T. Ishii, and K. Maeto. 2006. The use of arthropods as indicators of ecosystem integrity in forest management. Journal of Forestry.

Maleque, M. A., K. Maeto, S. Makino, H. Goto, H. Tanaka, M. Hasegawa, and A. Miyamoto. 2010. A chronosequence of understory parasitic wasp assemblages in secondary broad-leaved forests in a Japanese 'satoyama' landscape. Insect Conservation and Diversity **3**:143-151.

Marino, P., D. Landis, and B. Hawkins. 2006. Conserving parasitoid assemblages of North American pest Lepidoptera: Does biological control by native parasitoids depend on landscape complexity? Biological Contol **37**:173-185.

Marino, P. C., and D. A. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecological Applications **6**:276-284.

Matlock, R. B., and R. de la Cruz. 2003. Ants and indicators of pesticide impacts in banana. Environmental Entomology **32**:816-829.

Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. Science **277**:504-509.

McNaughton, S. J. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. The American Naturalist **111**:515-525.

Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003. Temporal variation in the response of parasitoids to agricultural landscape structure. Agriculture Ecosystems & Environment **96**:29-35.

Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999. Does agricultural landscape structure affect parasitism and parasitoid diversity? Ecological Applications **9**:634-641.

Merriam, G. 1988. Landscape dynamics in farmland. Trends in Ecology and Evolution **3**:16-20.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology **12**:39-45.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature **390**:507-509.

Naganuma, K., and H. A. Hespenheide. 1988. Behavior of visitors at insect-produced analogues of extrafloral nectaries on *Baccharis sarothroides* Gray. The Southwestern Naturalist **33**:275-286.

NCDC. 2009. National Climatic Data Center, National Oceanic and Atmospheric Administration. http://www.ncdc.noaa.gov/oa/ncdc.html.

Ohnesorg, W. J., K. D. Johnson, and M. E. O'Neal. 2009. Impact of reduced-risk insecticides on soybean aphid and associated natural enemies. Journal of Economic Entomology **102**:1816-1826.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology **10**:99-109.

Paoletti, M. G. 1999. Arthropods as bioindicators in agroecosystems of Jiang Han Plain, Quianjiang City, Hubei China. Critical Reviews in Plant Sciences **18**:457-465.

Pfiffner, L., and H. Luka. 2000. Overwintering of arthopods in soils of arable fields and adjacent semi-natural habitats. Agriculture Ecosystems & Environment **78**:215-222.

Pisani-Gareau, T., and C. Shennan. 2010. Can hedgerows attract beneficial insect and improve pest control? A study of hedgerows in Central Coast farms. The Center for Agroecology and Sustainable Food Systems, University of California, Santa Cruz, California.

Rao, R. S. P., and M. K. S. Girish. 2007. Road kills: Assessing insect casualties using flagship taxon. Current Science **92**:830-837.

Rauwald, K. S., and A. R. Ives. 2001. Biological control in disturbed agricultural systems and the recovery of parasitoid populations. Ecological Applications **11**:1224-1234.

Ricarte, A., M. A. Marcos-Garcia, and C. E. Moreno. 2011. Assessing the effects of vegetation type on hoverfly (Diptera: Syrphidae) diversity in a Mediterranean landscape: implications for conservation. Journal of Insect Conservation **15**:865-877.

Riechert, S. E. 1998. The Role of Spiders and Their Conservation in the Agroecosystem. Pages 211-237 *in* R. Bugg, editor. Enhancing Biological ControlL Habitat Management to Promote Natural Enemies of Agricultural Pests. University of California Press, Berkeley, CA.

Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. Annual Review of Ecology Evolution and Systematics **38**:713-737.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs **43**:94-125.

Roschewitz, I., M. Hucker, T. Tscharntke, and C. Thies. 2005. The influence of landscape context and farming practices on parasitism of cereal aphids. Agriculture, Ecosystems and Environment **108**:218-227.

Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia **96**:439-449.

Rusch, A., M. Valantin-Morison, J. P. Sarthou, and J. ROger-Estrade. 2011. Multi-scale effects of landscape comlexity and crop management on pollen beetle parasitism rate. Landscape Ecology **26**:473-486.

Saaksjarvi, I. E., K. Ruokolainen, H. Tuomisto, S. Haataja, P. V. A. Fine, G. Cardenas, I. Mesones, and V. Vargas. 2006. Comparing composition and diversity of parasitoid wasps and plants in an Amazonian rain-forest mosaic. Journal of Tropical Ecology **22**:167-176.

Sarkar, S., and C. Margules. 2002. Operationalizing biodiversity for conservation planning. Journal of Bioscience **27**:299-308.

SAS. 2003. The SAS Institute, Inc., Cary, North Carolina.

Schmidt, M. H., A. Lauer, T. Purtauf, C. Thies, M. Schaefer, and T. Tscharntke. 2003. Relative importance of predators and parasitoids for cereal aphid control. Proceedings of the Royal Society of London B.

Shaw, M. R. 2006. Habitat considerations for parasitic wasps (Hymenoptera). Journal of Insect Conservation **10**:117-127.

Shelton, A., J. Andalcro, and J. Bardnard. 1982. Effects of cabbage looper, imported cabbage worm, and diamondback moth on fresh market and processing cabbage. Journal of Economic Entomology **75**:742-745.

Siriwong, W., K. Thirakhupt, D. Sitticharoenchai, J. Rohitrattana, P. Thongkongowm, M. Borjan, and M. Robson. 2009. DDT and derivatives in indicator species of the aquatic food web of Rangsit agricultural area, Central Thailand. Ecological Indicators **9**:878-882.

Skillen, E. L., J. Pickering, and M. J. Sharkey. 2000. Species richness of the Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) along a latitudinal gradient in eastern North American old-growth forests. Environmental Entomology **29**:460-466.

Snyder, W. E., and A. R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. Ecology **84**:91-107.

Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. 2006. Predator biodiversity strengthens herbivore suppression. Ecology Letters **9**:789-796.

Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. Ecology **82**:1571-1583.

Soluk, D. A., D. S. Zercher, and A. M. Worthington. 2011. Influence of roadways on patterns of mortality and flight behavior of adult dragonflies near wetland areas. Biological Conservation **144**:1638-1643.

Southwood, T. R. E. 1977. Habitat, the template for ecological strategies? The Journal of Animal Ecology **46**:337-365.

Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. Ecological Entomology **27**:631-637.

Straub, C. S., D. L. Finke, and W. E. Snyder. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? . Biological Control **45**:225-237.

Straub, C. S., and W. E. Snyder. 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. Ecology **87**:277-282.

Straub, C. S., and W. E. Snyder. 2008. Increasing enemy biodiversity strengtens herbivore suppression on two plant species. Ecological Applications **89**:1605-1615.

Sutherland, W. J., R. Aveling, L. Bennun, E. Chapman, M. Clout, I. M. Cote, M. H. Depledge, L. V. Dicks, A. P. Dobson, L. Fellman, E. Fleishman, D. W. Gibbons, B. Keim, F. Lickorish, B. B. Lindenmayer, K. A. Monk, K. Norris, L. S. Peck, S. V. Prior, J. P. W. Scharlemann, M. Spalding, and A. R. Watkinson. 2012. A horizon scan of global conservation issues for 2012. Trends in Ecology and Evolution **27**:12-18.

Thies, C., I. Roschewitz, and T. Tscharntke. 2005. The lanscape context of cereal aphid-parasitoid interactions. Proceedings of the Royal Society B **272**:203-210.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos **101**:18-25.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2008. Interannual landscape changes influence plant-herbivore-parasitoid interactions. Agriculture Ecosystems & Environment **125**:266-268.

Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. Science **285**:893-895.

Tilden, J. W. 1951. The insect associates of *Baccharis pilularis de candolle*. Microentomology **16**:149-188.

Townes, H. 1969. Genera of Ichneumonidae. American Entomological Institute, Ann Arbor, Michigan.

Townes, H. 1972. A light-weight Malaise trap. Entomological News **83**:239-247.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. vanNouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control **43**:294-309.

Tscharntke, T., A. CGathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natual enemies: community structure and interactions. Journal of Applied Ecology **35**:708-719.

UCIPM. 2007. Biological control and natural enemies. University of California Statewide Integrated Pest Management Program http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn74140.html.

USDA. 2008. Data sets: Table 10-Certified organic vegetable acreage, by State, 2005. Economic Research Service of the U.S. Department of Agriculture http://www.ers.usda.gov/Data/Organic/.

USDA. 2009. 2007 Census of Agriculture, 2008 Organic Production Survey. http://www.agcensus.usda.gov/. National Agricultural Census Bureau, United States Department of Agriculture.

van Nouhuys, S., and I. Hanski. 2002. Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. The Journal of Animal Ecology **71**:639-650.

Vattala, H. D., S. D. Wratten, C. B. Phillips, and F. L. Wackers. 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. Biological Control **39**:179-185.

Vollhardt, I. M. G., T. Tscharntke, F. L. Wackers, F. J. J. A. Bianchi, and C. Thies. 2008. Diversity of cereal aphid parasitoids in simple and complex landscapes. Agriculture Ecosystems & Environment **126**:289-292.

Wahl, D. B., and M. J. Sharkey. 1993. Superfamily Ichneumonoidea.*in* H. Goulet and J. T. Huber, editors. Hymenoptera of the World: An Identification Guide to Families. Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, Ontario.

Werling, B. P., T. D. Meehan, C. Gratton, and D. A. Landis. 2011. Influence of habitat and landscape perenniality on insect natural enemies in three candidate biofuel crops. Biological Control **59**:304-312.

WFA. 2005. Wild Farm Alliance http://www.wildfarmalliance.org/about/index.htm.

Wiedenmann, R. N., and J. W. SmithJr. 1997. Attributes of natural enemies in ephemeral crop habitats. Biological Control **10**:16-22.

Wilby, A., S. C. Villareal, L. P. Lan, K. L. Heong, and M. B. Thomas. 2005. Functional benefits of predator species diversity depend on prey identity. Ecological Entomology **30**:497-501.

Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems. Biological Contol **10**:4-15.

Woltz, J. M., R. Isaacs, and D. A. Landis. 2012. Landscape structure and habitat managment differentially influence insect natural enemies in an agricultural landscape. Agriculture Ecosystems & Environment **152**:40-49.