PROJECT REPORT

Final project report submitted to the Organic Farming Research Foundation:

Project Title:

Determining habitat requirements for natural enemies of crop pests

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OFRF funding: $8,770, awarded Spring 2007

Funding category: Research

Project period: 2007-2008

Report submitted: December 2009. 26 pages.

ORGANIC
FARMING
RESEARCH
FOUNDATION

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Determining habitat requirements for natural enemies of crop pests
Rebecca Chaplin-Kramer, University of California, Berkeley. December 2009.

Summary

Pest control by resident populations of natural enemies is influenced by the landscape context of the farm. Natural enemies, measured by weekly insect surveys, increased with the proportion of natural habitat in the surrounding landscape in all years of the study. Pest control function, assessed by a cage experiment, was also higher in more diverse landscapes. The effect of natural habitat on aphid distributions was not consistent across growing season or years, however. Identifying source habitat for aphids may be an equally important consideration in predicting aphid distributions as understanding the role played by their natural enemies.

Objectives

One of the Organic Farming Research Foundation's stated goals is to "take a systems-management (rather than an input-substitution) approach to solving production problems." This goal is exactly in line with my research: I am studying the mechanisms of natural pest control to promote systems management rather than input-substitution solutions to pest problems. Input-substitution approaches to pest control use organic pesticides in place of the more common conventional chemicals, which farmers have found time and again to be ineffective. Integrated pest management has made strides toward understanding how natural enemies of agricultural pests can control their populations, and research has focused mainly on augmentation techniques (releasing commercially-reared predators). However, this is still input-substitution; farmers have to continually buy these insects to release in their fields. A true systems-management approach identifies factors in the farm and the surrounding landscape that could promote stable resident populations of natural enemies. My research encapsulates this approach, by asking: how does the landscape surrounding the farm impact natural enemies and their ability to provide effective pest control?

Introduction

The intensification and expansion of agriculture in the latter part of the 20th century has amplified the age-old competition between humans and arthropod herbivores for food produced from crops. The recognition of the risks of pesticides has led the study of arthropod relationships at the interface of agricultural and natural systems in hopes of regaining aspects of natural pest control in our industrialized agriculture. Natural habitat near agricultural areas could provide resources for the natural enemies of agricultural pests, supplying these beneficial insects to farms to aid in pest control. Research in pest management has begun to focus on how landscape structure around farms affects natural enemy communities and the pest control services they provide on farm sites.

Across a range of cropping systems and natural enemy species, farms embedded in more complex landscapes (those with greater proportions of natural habitat) are associated with more abundant natural enemy populations[1] as well as more diverse natural enemy communities.[2] Natural enemy function, measured in rates of parasitism and predation, also increases with landscape complexity.[3] Through enhancements to natural enemy abundance, diversity, and function, complex landscapes may provide farms with improved pest control, depending on whether they also serve as a source of pests. Landscape studies have typically ignored the possibility that natural habitat may enhance pest populations as well as natural enemies. What farmers are really concerned about is not natural enemies per se, but the net effect on their pests. My research, however, examines the commingling variables of natural habitat affecting natural enemies affecting pests and natural habitat affecting pests directly.

Many experiments manipulating natural enemies densities under constant pest densities have demonstrated that greater abundance of natural enemies can help contain pest populations.[4] Removal of these key natural enemies results in dramatic explosions of pest populations.[5] Until recently, pest control studies did not include their experimental variables in a landscape context.[6] However, even the few landscape pest-control studies that exist have been correlative in nature, relating crop damage and natural enemy abundance to the landscape gradient but stopping short

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[1] Colunga-Garcia et al. 1997. Environmental Entomology **26**:797-804: Elliot et al. 2002. Biological Control **24**:214-220; Elliot et al. 2002. Environmental Entomology **31**:253-260; Frank and Riechart 2004. Bulletin of Entomological Research **94**:209-217; French et al. 2001. Environmental Entomology **30**:225-234; Letourneau and Goldstein 2001. Journal of Applied Ecology **38**:557-570; Menalled et al. 2003. Agriculture Ecosystems & Environment 96:29-35; Schmidt and Tscharntke 2005. Journal of Biogeography **32**:467-473.

[2] Buddle et al. 2004. American Midland Naturalist **151**:15-26; French and Elliot 2001. Southwestern Entomologist **26**:315-324; Kruess and Tscharntke 1994. Science **264**:1581-1584; Marino and Landis 1996. Ecological Applications **6**:276-284; Menalled et al.1999, Tscharntke et al. 1998, Tscharntke et al. 2002.

[3] Kruess 2003, Ostman et al. 2001, Menalled et al. 1999. Ecological Applications **9**:634-641; Thies et al. 2003. Oikos **101**:18-25; Thies et al. 2005. Proceedings of the Royal Society B-Biological Sciences **272**:203-210; Tscharntke et al. 1998. Journal of Applied Ecology **35**:708-719; Tscharntke et al. 2002. Ecological Applications **12**:354-363.

[4] Chang and Snyder 2004. Biological Control 31: 453-461; Ostman 2004. Biological Control **30**:281-287; Sunderland and Samu 2000. Experimentalis Et Applicata **95**:1-13.

[5] Cardinale et al. 2003. Ecology Letters **6**:857-865; Ostman et al. 2003. Ecological Economics **45**:149-158; Riechert and Bishop 1990. Ecology **71**:1441-1450; Schmidt et al. 2003. Ecology **77**:1975-1988.

[6] Thies and Tscharntke 1999. Science **285**:893-895; Thies et al. 2003. Oikos **101**:18-25.

of proving that natural enemies were the cause of the increased yield. My study bridges this gap, investigating both enemies and pests to determine the mechanisms governing pest abundance.

Materials and Methods

My research focuses on broccoli on California's Central Coast, where nearly half of the nation's broccoli is grown. Over 76,000 pounds of organophosphate insecticides and 2,900 pounds of carbamate insecticides are applied annually in Monterey County alone, causing significant threats to human health as well as contamination of several bodies of water in the Central Coast area, ultimately impacting such natural treasures as the Monterey Bay National Marine Sanctuary. Cabbage aphids (*Brevicoryne brassicae*) are a major pest of broccoli and can be controlled by natural enemies if not disrupted by pesticides. Important natural enemies of aphids include parasitic wasps (*Diaeretiella rapae*), lady beetles (Coccinellidae), lacewing larvae (Chrysopidae), spiders, and a variety of other coleopteran and hemipteran predators, though larvae of flies in the family Syrphidae are the most abundant aphid predator by far in broccoli. Adult syrphid flies are extremely mobile and search in many different habitats for aphid colonies on which to lay their eggs. This makes the surrounding habitat an important variable in their distribution on farms. Syrphid flies are especially vulnerable to pesticides and cannot be acquired commercially; they must migrate into the fields from surrounding areas. Syrphid flies are therefore an excellent study species to use to explore the effects of landscape on pest control.

My study is based on 16-18 organic broccoli farms in Santa Cruz, Monterey, and San Benito Counties. I conduct trials on organic farms because chemical pesticide applications disrupt the natural mechanisms I am trying to study. The farms were chosen to represent a gradient of landscapes, ranging from less than 5% to more than 80% natural habitat within a 3 km radius of the farm. Most of the farms are large-scale industrial organic operations, similar in most respects to conventional farming except for the use of chemicals. The few farms I have included that grow a more diverse array of vegetables in smaller quantities (including Earthbound's Carmel Valley farm, UC Santa Cruz's experimental farm, the USDA experimental farm, the Salinas farm for the Agricultural Land-Based Training Association, and Pinnacle Organic's Hollister and San Juan Ranches) occur on both ends of the landscape gradient.

The bulk of my research is composed of two main components: habitat mapping using ArcGIS and weekly insect surveys at each of the farms over the growing season in three separate years (2006-2008). Two other components have emerged out of questions raised by the insect surveys: a field experiment to measure pest control function at each end of the landscape gradient and lab experiments focusing on the physiological impacts of an alternate host plant for aphids.

GIS habitat mapping

Aerial photographs of 1m resolution were obtained through the National Agricultural Imagery Project (NAIP) for the 3 km area surrounding each farm site in each year. As production is often rotated among fields, it was not possible to reuse the same sites every year, so some updating was necessary between years, and in some cases new sites were acquired if certain producers chose not to grow broccoli in a given year. The photographs were digitized using an object-based image analysis program called E-Cognition, and the resulting maps were classified by hand into the following land-use categories: annual agriculture, perennial agriculture, fallow agriculture, industrial, residential, road, bare, water, and natural habitat. Natural habitat is in the process of being further broken down into classes such as riparian, grassland, deciduous woodland, coniferous woodland, wetland, and chaparral. Proportional areas were then computed for each land-use class at a radius of 500m, 1000m, 1500m, 2000m, 2500m, and 3000m around the farm site. These proportional areas were used in regression analysis of the insect surveys to determine which land-uses and which scales were most predictive of farm insect populations. This study will use the convention established by other studies in this field, using "landscape complexity" to describe the land-use gradient, with lower proportions of natural habitat (usually corresponding to higher proportions of agricultural habitat) as "simple" and higher proportions of natural habitat (or lower proportions of agricultural habitat) as "complex."

Insect surveys

Ten broccoli plants per week were collected at each field site starting five to six weeks before harvest and continuing until harvest. The plants were brought back to the lab to be washed over a sieve, and all insects collected were then identified and counted under the microscope. This method ensures that all the insects inhabiting a plant were detected, regardless of behavioral differences (for example, it has been suggested that syrphid larvae are primarily nocturnal and would not be detected in as high abundances from visual observation in the field). While it is possible that some of the more mobile, winged predators, such as adult lady beetles, could escape from the plant as it was being collected, at least some of these individuals were collected in this manner, and any bias in underestimating their abundance due to collection method is consistent across sites.

Plant mass was recorded in years 2007 and 2008, as the plants are so large (1.5-2 kg) toward harvest it became necessary to sub-sample in the final week or two. Therefore, data from 2007 and 2008 are analyzed in terms of insects per kilogram of plant matter, while data from 2006 are analyzed in terms of insects on the whole plant. For this reason, and because sites shifted around somewhat from year to year as previously noted, all three years were analyzed separately. As count data such as these are not normally distributed, a log-transformation was employed for all three years. Data were analyzed with a multiple regression of log-syrphids (2006) or log-syrphids/kg (2007, 2008) against landscape, age of planting, and date (since sites were not all planted at the same time). For demonstration purposes, data from 2007 and 2008 can be converted back to insects per plants by projecting average plant mass per site based on the mass of the plants sampled and the degree of sub-sampling (half plants or quarter plants). Despite the more appropriate use of log insect counts per plant or per kilogram for analysis, it is easier to understand insect counts per plant, so I will present the data both ways here.

Field experiment: pest control function

While the weekly insect surveys allow me to track distributions of aphids and their natural enemies over time, it is not possible to establish cause and effect from this method of observation. In order to determine whether changes in aphid populations are due to natural enemies as opposed to other exogenous factors (weather, dispersal patterns, sources of aphids), it is necessary to control for these other possible factors. A cage study was designed to hold initial densities of aphid constant across field sites so that population growth with and without predation could be compared in different landscapes. Four sites at the simpler (<15% natural habitat in 1500 meters) and four at the more complex (>50% natural habitat in 1500 meters) ends of the landscape gradient were selected. Sample size was constrained by farmer willingness to participate in the study and by the desire to achieve a meaningful difference by focusing on the extremes of the gradient.

Potted broccoli plants in individual cages were set out at each farm site in three replicate groups for 12 days. Each group had one closed cage, two open cages, and one sentinel cage, for a total of 12 cages per site (96 cages total). The cages were constructed out of a fine organdy mesh to allow sunlight, precipitation and wind to pass through relatively unencumbered, but to keep out parasitoids and other micro-enemies. Each cage sat on a plastic stage over a bucket of water, with cotton rope extending from the soil in the pot through the plastic stage into the water beneath it. In this way, the plants had sufficient access to water for the duration of the experiment. Dataloggers (Hygrochron I-buttons, Embedded Data Systems, Lawrenceburg, KY) recorded temperature and humidity in each of the treatments at each site to determine if there were any microclimate differences between treatments. No significant differences were found.

Broccoli plants in the open and closed cages were inoculated with 100 aphids each. Care was taken to select only non-winged morphs so that aphids would not leave the experimental plants, since this would confound the experiment and export unwanted pests to farmers' fields. The sentinel cages were identical to the open cages, but no aphids were placed on these plants. The closed cages served as the control, measuring the population growth of aphids over 12 days at each site in absence of predation. The open cages served as the experimental group, measuring the population growth of aphids when exposed to predation and/or parasitism. The sentinel cages were a secondary control, to account for the possibility of resident aphids settling on the experimental plants, since the open cages would allow additional aphids as well as natural enemies onto the plants. The open cages had more replicates because this group was expected to show the greatest variance in outcome (depending on whether and when natural enemies found the aphids on these plants), and 3 replicates per site did not seem adequate to account for this variance. Plants were harvested at the end of the 12 days and brought back to the lab to process as outlined in methods for insect surveys.

Laboratory experiments: physiological impacts of mustard

Brassicas have a sophisticated defense system to ward off herbivores, a glucosinolate-myrosinase complex that essentially comprises a "mustard-oil bomb"[7]. Cabbage aphids can sequester these glucosinolates from brassicas and avoid the toxic products resulting from the degradation of these compounds by encapsulating the enzyme myrosinase into crystalline microbodies. When the aphid body is damaged, volatile isothiocyanates are released through the hydrolysis of glucosinolate by myrosinase[8]. This toxic compound can deter or even kill predators, but aphids are only able to produce it when fed a diet high in glucosinolates, such as *Brassica nigra*[9]. Cultivated brassicas such as broccoli have much lower glucosinolate concentrations than their wild relatives and it is unclear whether aphids are capable of building this mustard bomb to the

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[7] Ratzka, A., H. Vogel, D. J. Kliebenstein, T. Mitchell-Olds, and J. Kroymann. 2002. Proceedings of the National Academy of Sciences of the United States of America 99:11223-11228.

[8] Francis, F., G. Lognay, and E. Haubruge. 2004. Journal of Chemical Ecology 30:741-755.

[9] Kazana, E., T. W. Pope, L. Tibbles, M. Bridges, J. A. Pickett, A. M. Bones, G. Powell, and J. T. Rossiter. 2007. Proceedings of the Royal Society B-Biological Sciences 274:2271-2277.

same extent when feeding on broccoli. If not, mustard could be providing a refuge to aphids from their enemies, and, given the prevalence of this weed around agricultural areas, could be an important source of cabbage aphids to farm fields.

To determine the potential of weedy mustard to serve as a source of aphids to farms, a series of physiological laboratory experiments are currently being undertaken. First, glucosinolate content was measured in aphids fed broccoli (*Brassica oleracea*) vs. aphids fed mustard (*Brassica nigra*) using High-Performance Liquid Chromatography in collaboration with a lab at UC Davis (Dan Kliebenstein, Dept. of Plant Sciences). Aphids were collected from colonies reared on broccoli or mustard in the greenhouse.

Next, ongoing feeding trials measure the daily rate of aphid consumption by syrphids and syrphid mortality to determine whether aphids are safer from predation when feeding on mustard than on broccoli. Immediately upon hatching, syrphid larvae are placed in a petri dish on either a broccoli leaf or a mustard leaf, with aphids from colonies reared on the corresponding plants. Each day, the number of aphids remaining is recorded, aphids are replenished to ensure a sufficient amount for the syrphid to reach satiation (ranging from 10 to 100 aphids, depending on the age of the syrphid), and the leaf is replaced to maintain freshness. This process continues until the syrphid dies or pupates, and if pupation occurs, the adult that emerges is saved for later species identification.

Finally, aphid growth and reproduction experiments have been initiated to determine whether aphids incur a physiological cost of building the mustard bomb, in the form of slower development or lower fecundity. Several aphid adults are placed on a potted broccoli or mustard plant in a cage that clips directly onto the leaf surface without damaging it. The first day that nymphs are observed on the leaf, the adults are removed and the cohort of nymphs (F1) are tracked until first reproduction. The number of days until the next generation of nymphs (F2) is produced is recorded for that F1 cohort, and then each of the F1 aphids (now adults) are moved to their own leaves, each in a clip cage. Daily observations are made of the number of nymphs produced per aphid, and each day the nymphs are removed to remove any artifact of crowding from the effect of the cage. This continues until the F1 aphid dies, providing a measure of time to first reproduction as a proxy for development rate and total nymphs produced as a measure of lifetime fecundity.

Results and Discussion

Insect surveys

Syrphids showed a strong response to landscape complexity in all three years of the study, increasing significantly with natural habitat in the area surrounding the farm (Fig. 1, $r^2 = 0.21$, $p << 0.01$ for 2006; $r^2 = 0.35$, $p << 0.01$ for 2007; $r^2 = 0.37$, $p << 0.01$ for 2008). The metrics and scales at which these predators were most strongly correlated with landscape were not consistent from year to year, however. In the first year, proportion of non-crop habitat (which can include residential, and industrial land-uses in additional to natural habitat) was more predictive than proportion of natural habitat alone. In the second and third years, proportion of natural habitat was most predictive. In the first and third years, syrphids were most tightly correlated with landscape at a scale of 1000 meters, while in the second year the correlation was strongest at a scale of 2500 meters. Age of planting was also a significant factor ($p < 0.05$ in all years), with syrphids increasing toward harvest, but date during the growing season was not.

Natural enemy richness, measured as the number of different natural enemy taxa per site each week, also increased with natural habitat in 2007 and 2008 (Fig. 2, $r^2 = 0.28$, $p << 0.01$ for 2007; $r^2 = 0.43$, $p << 0.01$ for 2008), but this trend was not significant in 2006 ($p = 0.12$). Again, the relevant scales varied, 1000 meters being most predictive for natural enemies in 2008 and 2000 meters being most predictive in 2007. Plant age and date during the growing season were also significant factors in most years, as natural enemy communities grew more diversified over the time to harvest ($p < 0.01$ for 2006 and 2008; non-significant in 2007) and over the course of the summer ($p < 0.05$ for all years).

Parasitism was not correlated with landscape in any of the years (Fig. 3). This is an interesting result, as other studies have shown increased parasitism in addition to increased enemy abundance and richness in landscapes with greater landscape complexity[10]. This difference could be due to the fact that the complex end of the landscape gradient in this study contains far more natural habitat than most studies, and as specialist enemies, parasitoids may have a harder time finding their prey in too diverse of landscapes. Parasitism appears to peak in the mid-range of the landscape gradient, between 20 and 40% natural habitat in the surrounding 3000 meters. While parasitoids are reliant on flowering plants as nectar sources, they do not benefit from alternate prey and may therefore require less off-farm habitat than more generalist natural enemies.

The majority of studies investigating the effect of landscape on so-called pest control stop short of actually measuring the effect on the pests themselves. An increase in natural enemy abundance, richness, or activity (such as parasitism rate) is often taken as an indicator of increased pest control, without actually documenting a decrease in pest abundance or damage[11]. In this study, no significant effect of landscape complexity was found on aphids in 2006 or 2007, and in 2008 the trend found was the reverse of what was expected, aphids increasing slightly with proportion of natural habitat in 1500 meters of the farm (Fig. 4, $r^2 = 0.26$, $p < 0.05$). This analysis masks a temporal interaction with landscape, however, which is better illustrated by Figure 5. Breaking the landscape complexity down into categories reveals that aphid distributions behave more as expected towards the ends of the landscape than in the middle. Despite similar initial aphid densities, farms in “simple” landscapes (with less than 15% natural habitat in the surrounding 1500 meters) showed greater aphid increases for the latter half of the growing period than farms in “complex” landscapes (surrounded by more than 50% natural habitat) in all three years. As pest infestation becomes more problematic for farmers closer to harvest, this seems a relevant way to examine the data. The mid-range of the landscape gradient (20-50% natural habitat in 1500 meters) is more confounding; aphid densities exceeded those at

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[10] and [11] Kremen C. and R. Chaplin-Kramer. 2007. Insects as providers of ecosystem services: crop pollination and pest control. In Insect Conservation Biology: proceedings of the Royal Entomological Society's 23rd Symposium. (Stewart, A.J.A., New, T.R. and Lewis, O.T. (eds)) CABI Publishing, Wallingford, 349-382.

either end of the gradient in 2006 and 2008, while in 2007 aphid densities were lower until the final week before harvest, when there appeared to be a population explosion.

Using these somewhat arbitrary though useful categories to break down the landscape gradient can be helpful in elucidating further trends. Examining syrphid abundance and natural enemy richness in these landscape categories week by week reveals a similar trend as that found for the aphids. That is, the difference between syrphid densities (Fig. 6) and natural enemy diversity (Fig. 7) at the ends of the gradient is fairly pronounced in all three years, but measures for these natural enemies in the mid-range of the gradient do not necessarily fall neatly between the two extremes. Furthermore, as is seen with aphid densities, the difference between natural enemies at the two ends of the gradient changes over time. However, while for aphids the two ends of the gradient began with similar densities that grew faster at the simple (<15% natural habitat) end than the more complex (>50% natural habitat) end, the reverse appears to be true for natural enemies. Farms in complex landscapes had more syrphids and more diverse enemy communities in the first weeks of the growing period than those in simple landscapes in all three years and the two generally converged over time, with the simple landscapes closing the gap and sometimes even surpassing those complex landscapes by harvest time. This apparent lag-time in the appearance of natural enemies at the farms in simple landscapes may account for the greater aphid growth seen toward harvest at these sites. Aphid population growth is exponential in absence of predation and, if natural enemies do not arrive early enough in the establishment phase, aphid populations could easily grow beyond the point where enemies can contain them.

The effect of landscape on the response of syrphids to the previous week's densities of aphids is also an informative way to examine these data. It makes sense to compare syrphids in one week to aphids in the previous week, because the implicit hypothesis in studying pest control is that natural enemies arrive in response to pest densities, and therefore we would expect higher syrphid densities the week after seeing higher aphid densities. In 2008 and 2006, complex landscapes showed a much steeper response than simple landscapes; syrphids increased more for a given density of aphids in the previous week on farms in complex landscapes (Fig. 8; $r^2 = 0.47$, $p << 0.01$ for 2008; $r^2 = 0.17$, $p < 0.05$, with a landscape by aphid interaction of $p << 0.01$ for 2006). The difference was even more pronounced in 2006, when farms in simple and mid-range landscapes show a completely flat response with a similar number of syrphids regardless of the previous week's aphid densities. In 2007, the syrphid response to aphids has a similar slope in simple landscapes as in complex landscapes but the intercepts are offset such that there are nearly double the syrphids for a given density of aphids in complex landscapes as simple landscapes ($r^2 = 0.27$, $p << 0.01$). The mid-range landscapes again defy generalizations across years, showing a steeper slope than even the complex landscapes in 2008 and a shallower one than both simple and complex landscapes in 2006 and 2007.

While it becomes increasingly difficult to understand trends in the mid-range landscapes as the data are more closely examined, the contrast between the two extremes of the landscape gradient is fairly apparent. Farms in complex landscapes begin their growing period with greater natural enemy densities and diversity as compared to simple landscapes, a difference that is magnified by a stronger response to existing aphid populations in complex landscapes and which may account for higher aphid peaks toward harvest in simple landscapes despite potentially similar initial densities. However, two issues remain unresolved. The first is why the trend for aphid densities is only apparent at the ends of the landscape gradient, when syrphid densities and enemy richness both show fairly strong positive correlations with increasing landscape complexity. Aphid distributions are obviously governed by more factors than natural enemies alone, such as climate, wind patterns, and source habitat. It could be that these other mitigating factors overwhelm the effect of enemies on aphid populations in the mid-range landscapes. Identifying one possibility for an additional mitigating factor (source habitat) is the focus of the last section, on the physiological impacts of mustard. A second unresolved issue is that while slower natural enemy response may account for the near-harvest aphid peaks in simple landscapes, an observational study such as this one is inadequate to assign cause and effect. In order to truly determine whether natural enemies are better containing pests in complex landscapes as compared to simple landscapes, a manipulative experiment is needed. This is addressed in the following section, the field experiment assessing pest control function.

Field experiment: pest control function

Pest control was assessed at the site level by subtracting the average aphid densities on the sentinel plants from the average aphid densities on the plants in the open cages and dividing that by the aphid densities on the plants in the closed cages. Subtracting this value from 1 yields the proportional reduction in aphid densities due to pest control. Considering a relative measure such as pest reduction as opposed to final aphid densities controls for endogenous differences in aphid population growth rate at different sites. As aphid reproduction is strongly dependent on temperature, climatic differences between sites can result in vastly different growth rates. Comparing aphid population growth in the closed cages (free from predation) reveals this disparity, with sites ranging from a mere doubling of aphid densities over the 12 day study period to a ten-fold increase. These differences in reproductive rates were not related to landscape complexity.

Pest control provided by natural enemies in complex landscapes (>50% natural habitat) was nearly double that found in simple landscapes (<15% natural habitat), with pest suppression approaching (and at one site even exceeding) 100% in complex landscapes (Fig. 9a, single-factor ANOVA, $p << 0.01$). Pest suppression in excess of 100% means that the plants in the open cages had lower aphid densities than even the sentinel plants; that is, enemies were able to reduce not only the experimental aphid population, but they eliminated any naturally settling aphids as well. The sentinels most likely did not receive comparable pest control services because there was no initial aphid population to attract enemies to these plants early in the experiment.

While the effect of landscape complexity on pest control is significant, the variability is not consistent. As shown by the standard error bars in Fig. 9a, the error or statistical noise in the data for simple landscapes is more than twice that for complex landscapes. A closer inspection of the data reveals that two of the simple sites exhibited much greater pest reduction than the other two. Interestingly, this difference corresponds to a difference in local farm diversity. Although not a part of the intended experimental design, the sites within each landscape category break down neatly into two local categories: those with hedgerows adjacent to the field and diverse plantings (locally complex), and those lacking hedgerows and employing large-scale monoculture broccoli (locally simple). Reanalyzing the data along these lines (two-factor ANOVA with local and landscape complexity, see Fig. 9b) shows that there is a significant landscape effect ($p << 0.01$), a significant local effect ($p << 0.01$), and a significant interaction between the landscape and local scales of complexity ($p = 0.01$). Specifically (according to the Tukey test for Honest Significant Differences), there is no effect of local complexity in complex landscapes, but in simple landscapes, locally complex sites have nearly four times the pest reduction as locally simple sites ($p << 0.01$). Likewise, there is no effect of landscape complexity at locally complex sites, but at locally simple sites, complex landscapes show a similar four-fold pest control advantage over simple landscapes ($p << 0.01$). It appears that local complexity can compensate for a lack of landscape complexity or vice versa. In terms of pest control function, sites with high local complexity and low landscape complexity are indistinguishable from sites with low local complexity and high landscape complexity.

Caution must be exercised in the interpretation of this analysis due to the low sample size resulting from further breaking down the categories into local and landscape complexity. While 96 total cages stretched the limit of our logistical capacity and while four sites per landscape category was the maximum that could be acquired through farmer willingness to participate, adding the additional factor of local complexity reduces the effective sample size to 2 per group. Ameliorating this statistical concern may not be as straightforward as it sounds, however. Reducing within-site replication would compromise the integrity of the pest reduction measure, and changing the minds of farmers who were unwilling to participate would be difficult, considering their deep concerns about bringing pests (however well-contained) onto their farm. Therefore, it was not possible to increase landscape-level replication. Nonetheless, this experiment was repeated in summer 2009, and preliminary analysis suggests that this substitutability of local and landscape complexity is consistent across years.

Laboratory experiments: physiological impacts of mustard

This component of the study is an important consideration in helping to explain the apparent lack of a relationship between aphids and landscape complexity over the whole gradient. Examining the middle of the landscape gradient for possible sources of aphids would be an important next step in understanding the role of landscape in aphid distributions; however, before aphid sources can be mapped, they must first be identified, and wild mustard is a plausible candidate for an aphid source due to its potential to serve as an enemy-free refuge for this pest.

The first question is whether aphids feeding on mustard contain more glucosinolates, the building blocks for the mustard bomb, than aphids feeding on broccoli. The answer to this is a definitive yes. The chemical assays showed that mustard-fed aphids contain more than ten times the glucosinolates of broccoli-fed aphids (Fig. 10a, $p < 0.01$). While broccoli-fed aphids still have detectable levels of glucosinolates (as compared to the sugar-water-fed aphids in Kazana et al. 2007, which had none), it seems likely that the concentrations of these compounds are not high enough for aphids to build the mustard bombs to deter their enemies so effectively.

The next question is whether syrphids are less effective predators of aphids on mustard as a result of this greater glucosinolate content. Initial results indicate that the answer to this is also yes. Syrphids ate almost five times more broccoli-fed aphids over their entire larval development than mustard-fed aphids (Fig. 10b, $p < 0.01$) and three times as much at their maximum (Fig. 10c, $p < 0.01$). But the most impressive result to come out of this study so far is the impact on larval development. Figure 11 shows average aphid consumption on a daily basis by syrphids on these two food sources, and the line for mustard clearly ends well before the line for broccoli. This is not because syrphids consuming mustard-fed aphids pupated more rapidly than syrphids on the broccoli-fed aphid diet, but rather, because no syrphids in the mustard treatment have survived to pupation at all! Syrphid mortality in the broccoli treatment was around 40%, while mortality in the mustard treatment is 100%. Although a syrphid larva is more or less confined to the plant it is born on (unless that plant is touching another, allowing the syrphid to move across), it seems likely that such high mortality rates would lead to fairly dramatic selection pressure against ovipositing on mustard. Rather than experiencing this kind of mortality in the field, it is possible that adult syrphid flies simply avoid mustard altogether.

The final question is whether aphids trade off a physiological cost in exchange for building the mustard bomb. If aphids develop more slowly or reproduce less on mustard, it may counteract any potential effect of reduced mortality from predation, leading to a net neutral effect of mustard. If aphids are attracted to the mustard as a refuge from enemies but develop or reproduce more slowly there than when on broccoli, mustard could even be considered a sink rather than a source of aphids, and could be drawing pests away from the crop. If, on the other hand, aphid development and/or reproduction are not hindered by mustard and aphid population growth on mustard is less impacted by mortality from predation, then mustard could indeed be serving as a source of aphids to crops. The aphid development studies are underway, and indicate that another consideration may come into play besides length of development until reproduction and total lifetime fecundity: production of winged morphs. Aphids generally trigger production of winged morphs through hormonal signals in response to over-crowding, giving birth to nymphs that will develop into winged adults that can seek out plants with fewer aphids to begin a new colony. Poor food quality can also serve as signal to produce winged morphs, since over-crowding usually reduces food quality of the plant (through depletion of important nutrients or stressing the plant to the point of wilting). Initial observations suggest that aphids on mustard may be producing more winged aphids than aphids on broccoli, perhaps in response to the higher glucosinolate content of mustard that may render it lower quality food in the eyes of aphids. This could mean that even with slower development or reproduction, mustard could be producing a greater total number of winged individuals than broccoli and thus serve as a greater exporter of aphids. This possibility will need to be taken into account when assessing mustard's potential as a source of aphids.

Impact of Results

The results of this project demonstrate that natural habitat does indeed provide a pest control service to farms. The insect surveys show that natural enemy abundance and diversity increases with landscape complexity, that syrphid response to aphids is fastest in the most complex landscapes, and that aphids reach higher population levels toward harvest in the simplest landscapes. The cage study quantifies the increased level of pest control in complex as compared to simple landscapes, although it also indicates that there is some degree of substitutability of local complexity for landscape complexity. The mustard experiments reveal the potential for this alternate host plant to provide a refuge to aphids from syrphid predation and ongoing studies will conclude whether weedy mustard around farms could serve as a host of aphids to crops.

While this research has established that a substantial amount (>50%) of natural habitat in the surrounding landscape essentially doubles the pest control found on farms without much nearby natural habitat (<15%), quantifying the amount of habitat necessary for a given level of pest control service, as stated in the objectives, is another matter. Specifically, what could be most useful about this application is determining whether any thresholds exist, whether a certain level of landscape complexity is necessary to achieve viable pest control (as defined by the growers' tolerance of aphid levels). To identify possible thresholds in the relationship between landscape complexity and pest control, the pest control experiment would need to be replicated across the entire landscape gradient, not just at the extremes. Given that the mid-range of the landscape gradient is where the trend tended to break down in the insect surveys, it may be more difficult to accomplish this than previously anticipated. Therefore, honing in on the confounding factors in the mid-range of the gradient, such as potential sources of aphids, is necessary before any threshold effects will be detectable.

Economic Analysis

It is anticipated that an economic analysis could at some point be performed weighing the costs and benefits to agriculture of proximity to natural habitat, but there is currently insufficient data to do so. Evidence so far suggests a benefit of increased pest control to farmers who are closer to natural habitat. The costs of creating and maintaining this natural habitat, however, would most likely be borne by the community, who would also benefit from fewer artificial pesticides in the environment. Depending on the results of future research, this approach may allow farmers to reduce their overall risk: as proximity to natural predators could allow for a low level of pests ever year, it would better defend against an acute and catastrophic outbreak. Future research will more accurately address these questions and will give farmers and our communities the data necessary to perform these cost-benefit analyses.

Publications/Outreach

My Ph.D. dissertation is the main publication emerging from this project, and is as yet still in progress. I anticipate at least four papers will come from this dissertation research: one on the landscape surveys, one on the pest control experiment, one on the mustard physiological work, and one from a meta-analysis comparing all currently published studies investigating landscape and pest control in order to draw some generalizations beyond this study system. I have been and intend to continue to be active in disseminating the results of my research to academic and professional audiences. I presented a poster at the Annual Meeting of the Ecological Society of America in 2007 and gave oral presentations at the same meeting in 2008 and 2009. I was interviewed on my work by the Environ Foundation (video footage should be forthcoming on http://www.environcorp.com/foundation) and by National Geographic News (http://news.nationalgeographic.com/news/2009/08/090812-killer-bugs-crops-pests.html).

I have participated in several farmer education programs at one of my field sites, the Agricultural Land-Based Training Association in Salinas—I presented hour-long lectures on the fundamentals of Integrated Pest Management as part of their Farmer Education Program in 2008 and 2009, and also participated in a field day sharing current and ongoing research with farmers in the broader community. I also plan to present my findings at Eco Farm, an annual meeting of agroecology researchers and agricultural professionals in Monterey in 2010. I have been fairly well connected with extension agents in Salinas as well as Davis and plan to plug into their outreach networks as I finish up my dissertation in 2010 and find more opportunities to address growers. Of course, the farmers I work with are my first audience. Every year, I provide them with a progress report, and at the end of my dissertation, I plan to engage them with a more exhaustive report that helps put their farm in context of the broader study and the landscape around them.

Farmer Adoption

Over the course of this research I have worked with a dozen or so farmers who at different times have several thousand organically certified acres under production. While I often chat with them informally during my field research, proximity to natural habitat is outside the control of these individual farmers. Nonetheless, there are several different approaches that might encourage a greater agricultural reliance on natural pest control:

Public Investment

Much of the natural habitat surveyed in this research is owned and/or managed by public agencies. Natural pest control provides a public benefit through a reduction in pesticides so one possible application of this research would be to encourage increased public conservation of natural habitat near farmlands. It is possible to form broad coalitions in support of this kind of conservation work with benefits flowing to farmers, who would need to spray fewer pesticides; to farm workers, who would be exposed to fewer pesticides; to conservationists, who would be able to preserve wild biodiversity; and to recreational users, who could have access to the natural habitat for hiking and fishing.

The Market for Farm Real Estate

If the ultimate results of this research do show a quantifiable financial benefit to farms near natural habitat, we could expect to see higher fees paid for this farmland and a similar drop in value for farmland far from natural habitat. This kind of realignment of real estate values would incorporate costs that had been external to the market and encourage more economically rational decisions about land use.

Hedgerows and Farm Diversity

While not an intentional focus of this research project, the serendipitous addition of a local component indicates a certain amount of substitutability for landscape-level complexity potentially provided by local complexity such as hedgerows, weed strips, and crop diversity. A second year of data collection in the early and late season for this pest control experiment was carried out in summer of 2009 and further analysis is necessary before conclusions can be published. The results so far seem to indicate that hedgerows and other on-farm modifications could magnify the populations of natural predators in the broader landscape. There seems to be some degree of interaction in complexity across scales. While several of the farmers in my study already use hedgerows in their management strategies, this could be an added incentive for other farmers to adopt this practice.

Areas Needing Additional Study

The major question raised by my research is the potential and significance of mustard as a source of aphids. The next steps for the determining the extent to which mustard serves as an enemy-free refuge and consequent aphid source contain both laboratory and field elements. In the lab, the feeding trials should be repeated for different natural enemies. While syrphids are the most conspicuous and arguably most important enemies in broccoli, there may be shifts in enemy community composition on mustard. What seems to be fairly conclusive evidence that mustard provides a syrphid-free refuge to aphids does not indicate that it will be enemy-free, or even enemy-reduced. The role of specialist parasitoids in particular should be investigated, for although they do not appear to be capable of containing aphid populations on broccoli, their specialized relationship with the cabbage aphid may promote them to a more important role in mustard. They may have evolved a means of dismantling the mustard bomb that other more generalist enemies lack. The feeding trials as described for syrphids cannot be replicated exactly for parasitoids, since an individual parasitoid consumes only one aphid in its lifetime. However, an experiment could be conducted that would release adult parasitoids into colonies of aphids on broccoli and on mustard with initially similar densities and record parasitism rates over time. Adult parasitoid fecundity is dependent in large part on the quality of larval food source, so a lower rate of parasitism on mustard colonies of aphids would indicate that the mustard bomb is effective at deterring even these specialist enemies.

Additionally, aphid populations on mustard should be located in the field and similar insect surveys to those performed on broccoli should be conducted to identify which enemies are present on mustard and how this community compares in abundance (relative to number of aphids) and diversity to the enemy community on broccoli. While the lab feeding trials can determine the degree of pest control that natural enemies are capable of when forced to feed on mustard aphids, only field surveys will reveal whether these enemies are actively avoiding mustard. They may arrive in equal numbers and simply consume less or they may not arrive at all, rendering mustard even more of a refuge from enemies than expected from the lab experiments. On the other hand, the community could simply shift to individuals capable of dismantling the mustard bomb, which could reduce or eliminate mustard’s status as a refuge for pests. Field surveys will help determine which of these possibilities is most likely.

The outcome of the aphid development experiments will help determine the research direction proceeding from here. Depending on the trade-offs between aphid development, reproduction, and production of winged morphs, more lab studies may need to be conducted to further elucidate the interplay of these factors. Another potential study to evaluate mustard as a source of aphids is a host choice experiment, measuring aphid preference for broccoli or other brassica crops in comparison to the higher-glucosinolate brassicas such as mustard. Winged aphids released into cages containing both broccoli and mustard would establish whether aphids are more attracted to one food source or the other. Another test would be to place directional traps around mustard in the field, measuring aphid movement to and from mustard to confirm whether mustard is in fact a net importer or exporter of aphids. When combined with information about development and reproduction on mustard and broccoli, these experiments would help determine the extent to which mustard may serve as a source, sink, or neutral space for aphids in agricultural landscapes.

If mustard is identified as a source of aphids in the landscape, the final piece of the puzzle would be to bring this information back into the insect survey data as another factor in the multiple regression. Although mustards are annuals that shift in local distribution and abundance from year to year, the types of habitat where they may be found are likely to be conserved at the landscape level. Potential mustard habitat could be identified in lieu of actual mustard patches, since this data was not acquired for the summers of 2006 though 2008. Field surveys would help determine the best candidates for potential mustard habitat. These habitat types could then be coded in the GIS maps and used to reanalyze the insect surveys to see if proportion of potential mustard habitat helps explain more of the variation in aphid distributions.

Part of the confusion in predicting aphid distributions especially in the mid-range of the landscape gradient could be that “natural habitat” contains some vegetation types that may serve as sources of natural enemies as well as other vegetation types that may serve as sources of pests—and some that may serve as sources of both! Splitting up the natural habitat category into different vegetation classes could help clarify the role of landscape in determining aphid distributions. This could entail classifying natural habitat into sub-classes that include mustard and non-mustard habitat, and would also likely involve discriminating between classes with good floral resources for natural enemies (such as chaparral, deciduous forest, and riparian habitat) and classes with poorer resources for natural enemies (such as coniferous forest and grassland). Although wind patterns and climate will still play a role in aphid colonization and population growth, more precise landscape information will almost certainly improve our understanding of these pest distributions. Wind and climate are more or less out of our control, but if we can understand how landscape impacts pest control, we can potentially alter it to serve our interests. We are still in the beginning stages of achieving the level of understanding necessary to make such land-use decisions. Continuing this line of research is vital to the goal of achieving a natural and sustainable means of pest control.

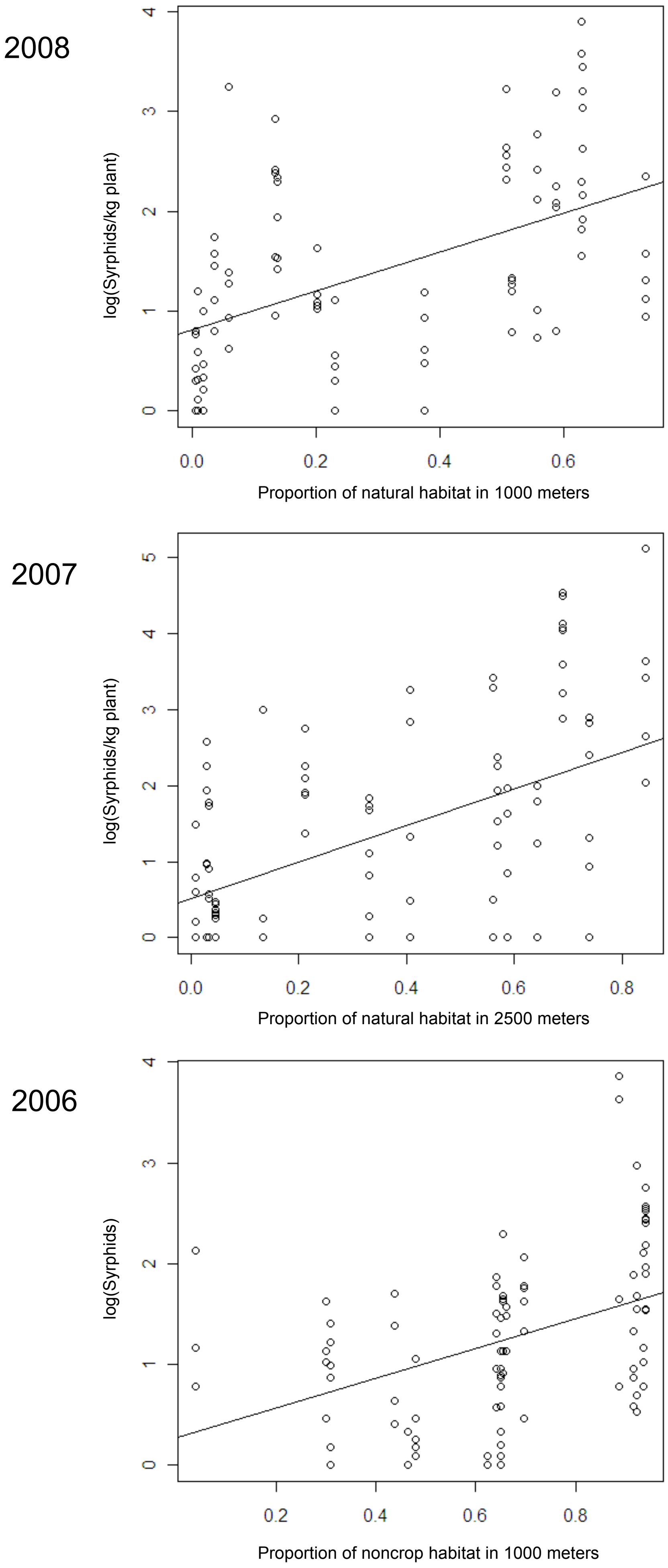
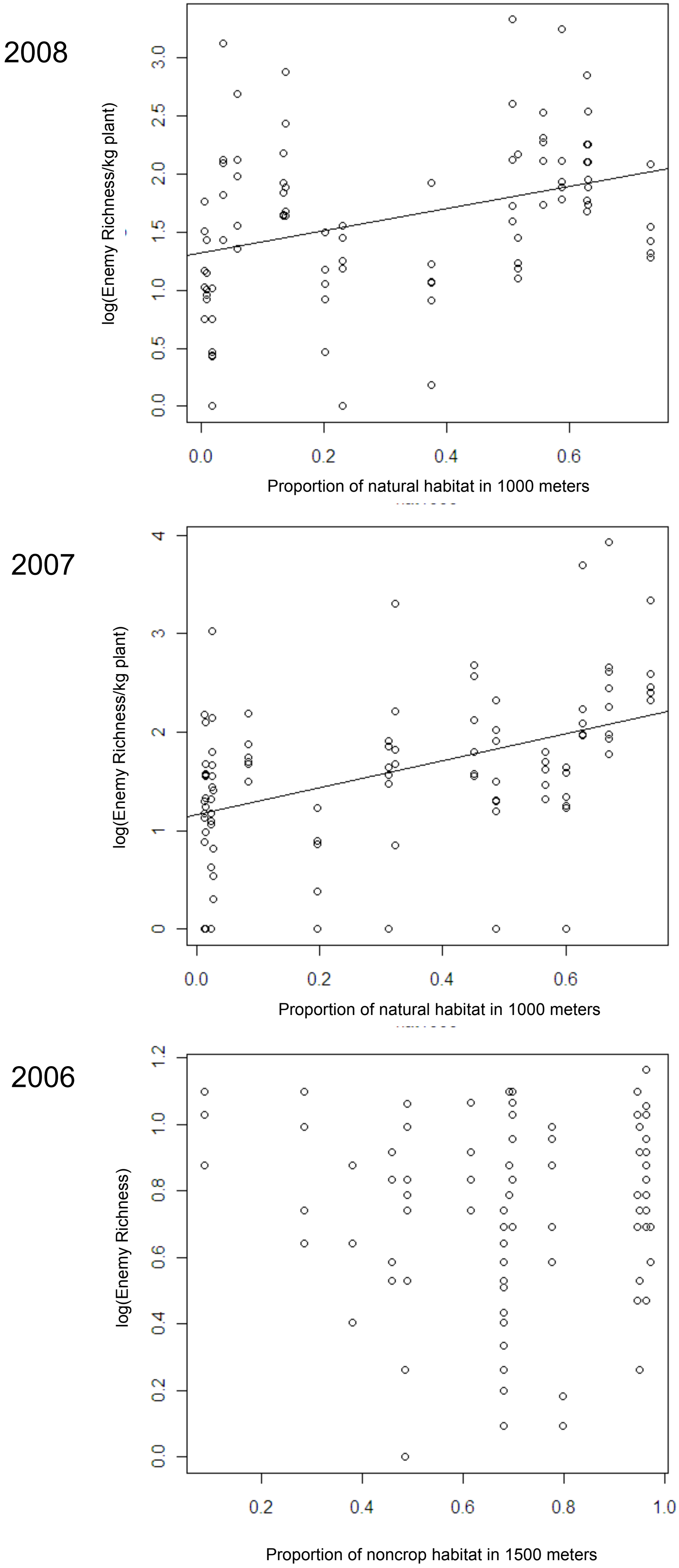

2008
log(Syrphids/kg plant)
0
1
2
3
4
0.0
0.2
0.4
0.6
Proportion of natural habitat in 1000 meters
2007
log(Syrphids/kg plant)
0
1
2
3
4
5
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 2500 meters
2006
log(Syrphids)
0
1
2
3
4
0.2
0.4
0.6
0.8
Proportion of noncrop habitat in 1000 meters

Figure 1



2008

2007

2006

Figure 2

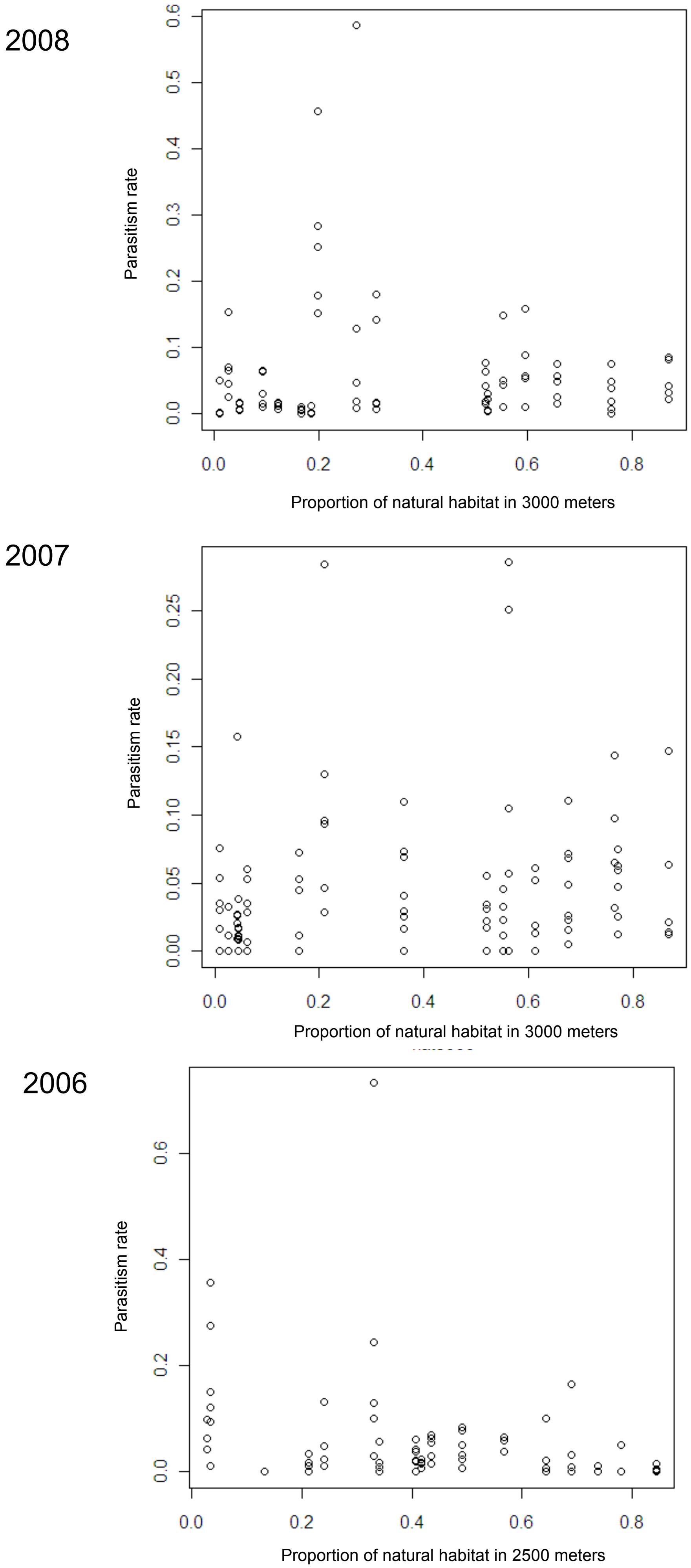

2008
Parasitism rate
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 3000 meters
2007
Parasitism rate
0.00
0.05
0.10
0.15
0.20
0.25
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 3000 meters
2006
Parasitism rate
0.0
0.2
0.4
0.6
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 2500 meters

Figure 3

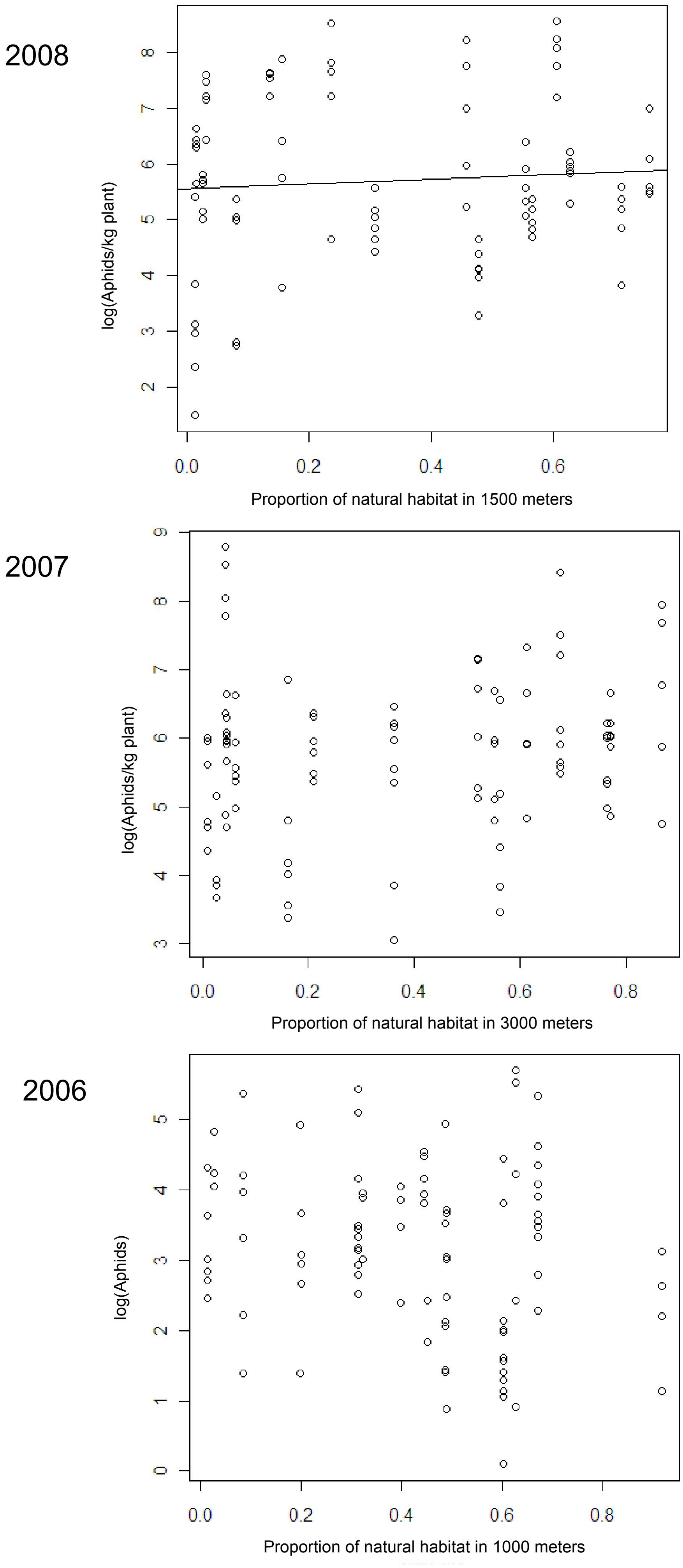
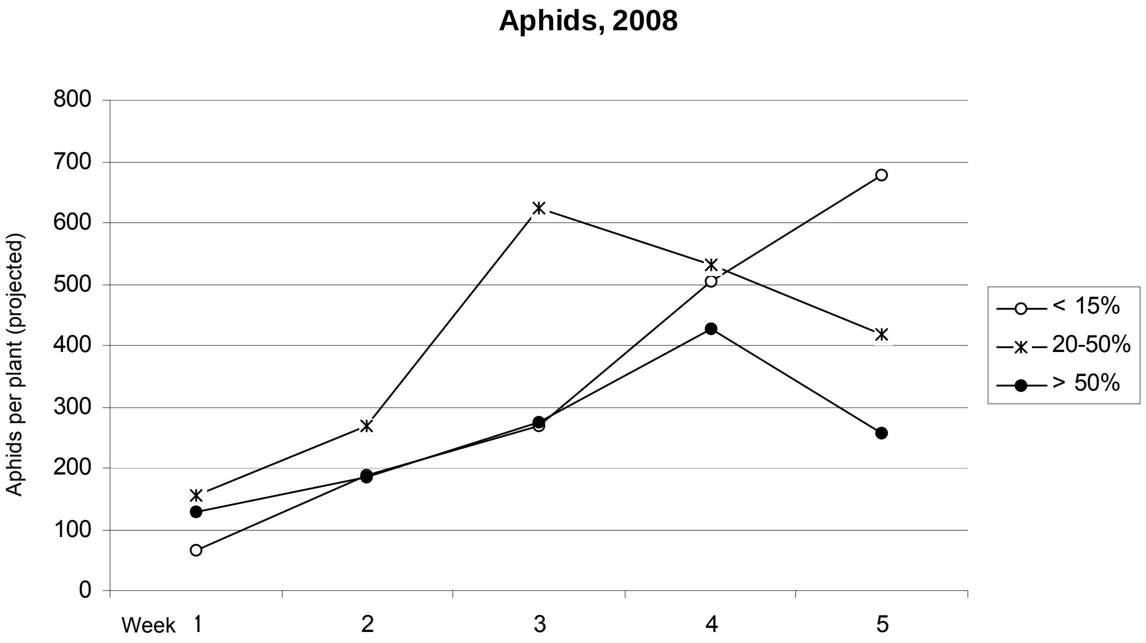
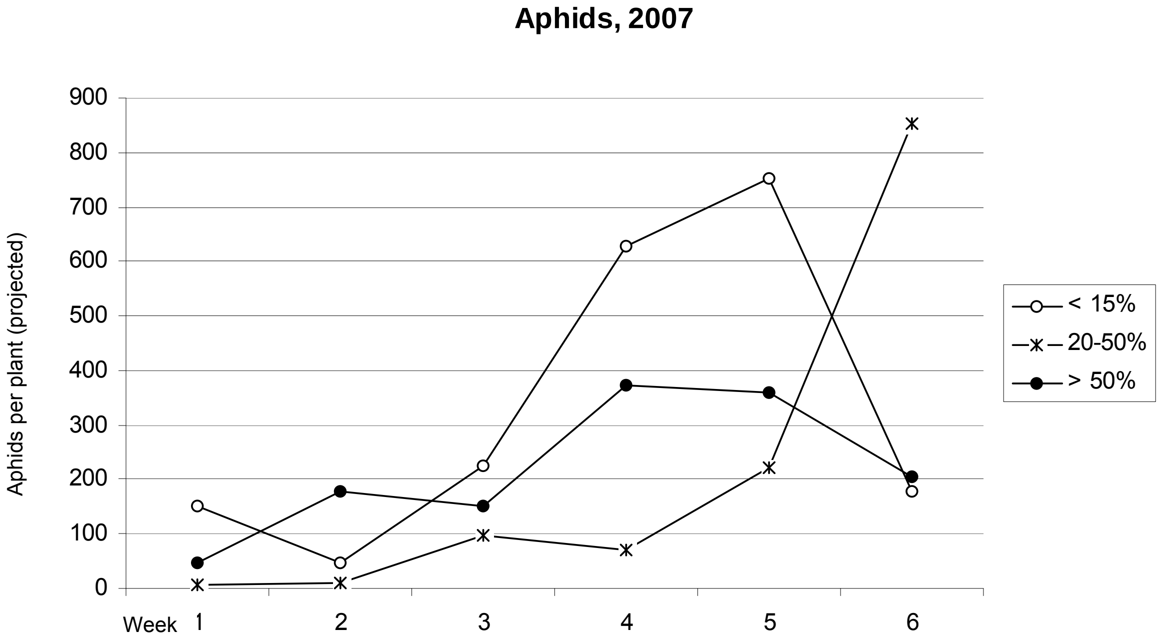

2008
log(Aphids/kg plant)
2
3
4
5
6
7
8
0.0
0.2
0.4
0.6
Proportion of natural habitat in 1500 meters
2007
log(Aphids/kg plant)
3
4
5
6
7
8
9
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 3000 meters
2006
log(Aphids)
0
1
2
3
4
5
0.0
0.2
0.4
0.6
0.8
Proportion of natural habitat in 1000 meters

Figure 4


Aphids, 2008
Aphids per plant (projected)
800
700
600
500
400
300
200
100
0
Week 1
2
3
4
5
< 15%
20-50%
> 50%


Aphids, 2007
Aphids per plant (projected)
900
800
700
600
500
400
300
200
100
0
Week 1
2
3
4
5
6
< 15%
20-50%
> 50%

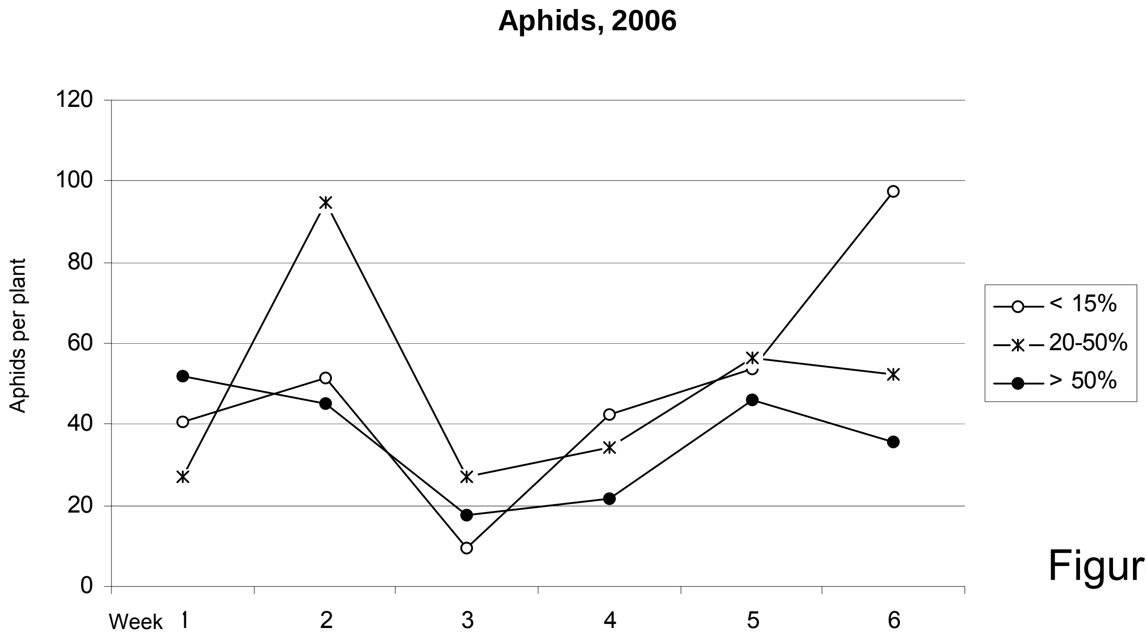
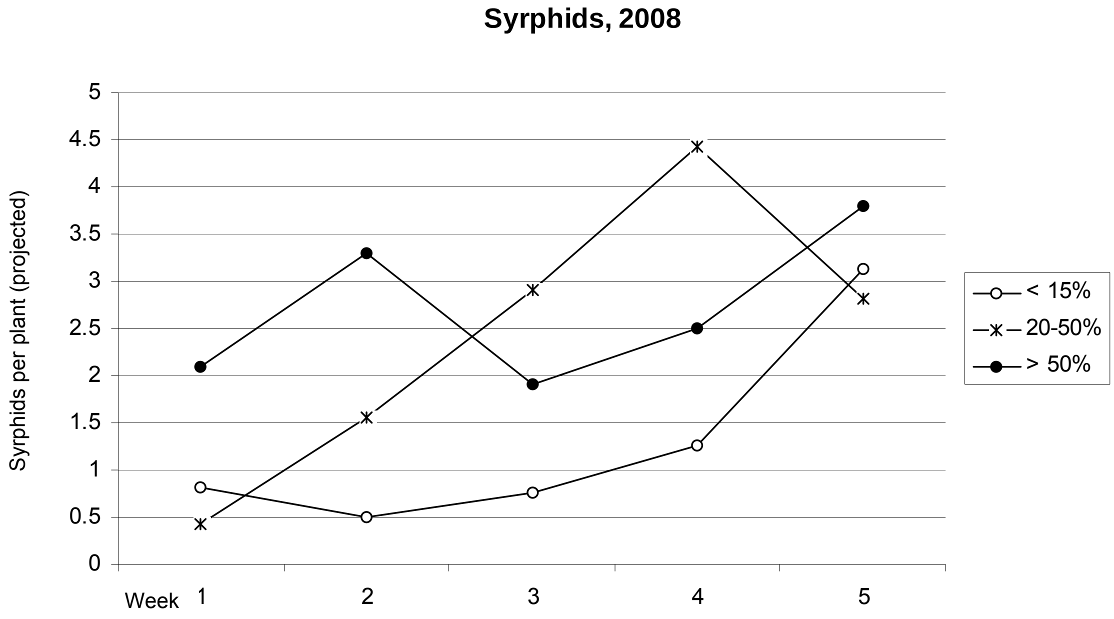
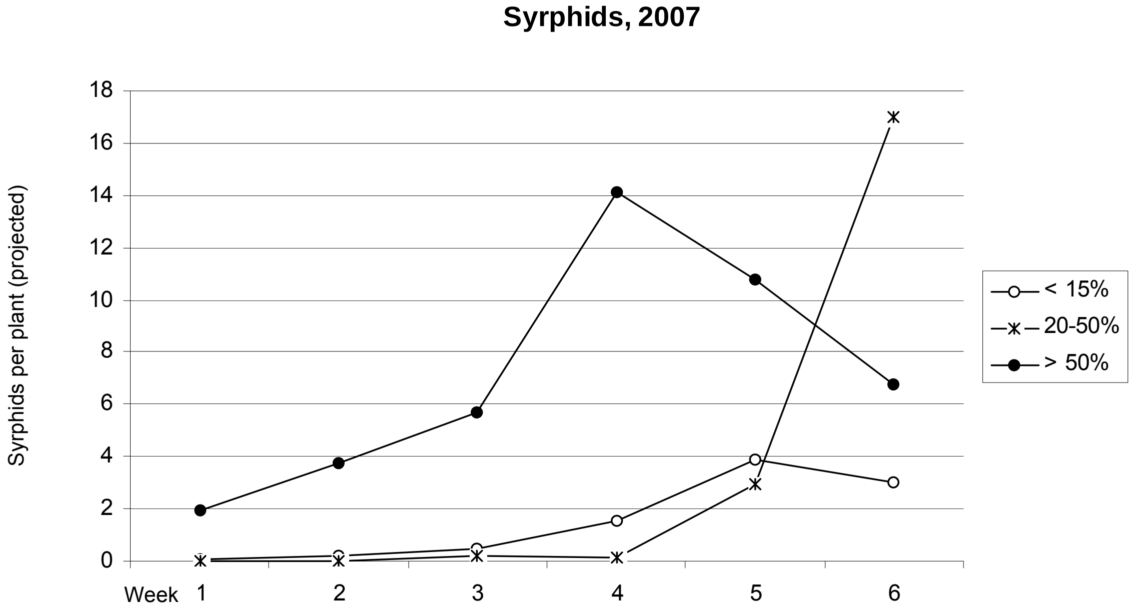

Aphids, 2006
Aphids per plant
120
100
80
60
40
20
0
Week 1
2
3
4
5
6
< 15%
20-50%
> 50%

Figure 5


Syrphids, 2008
Syrphids per plant (projected)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
Week
1
2
3
4
5
< 15%
20-50%
> 50%


Syrphids, 2007
Syrphids per plant (projected)
0
2
4
6
8
10
12
14
16
18
Week
1
2
3
4
5
6
< 15%
20-50%
> 50%

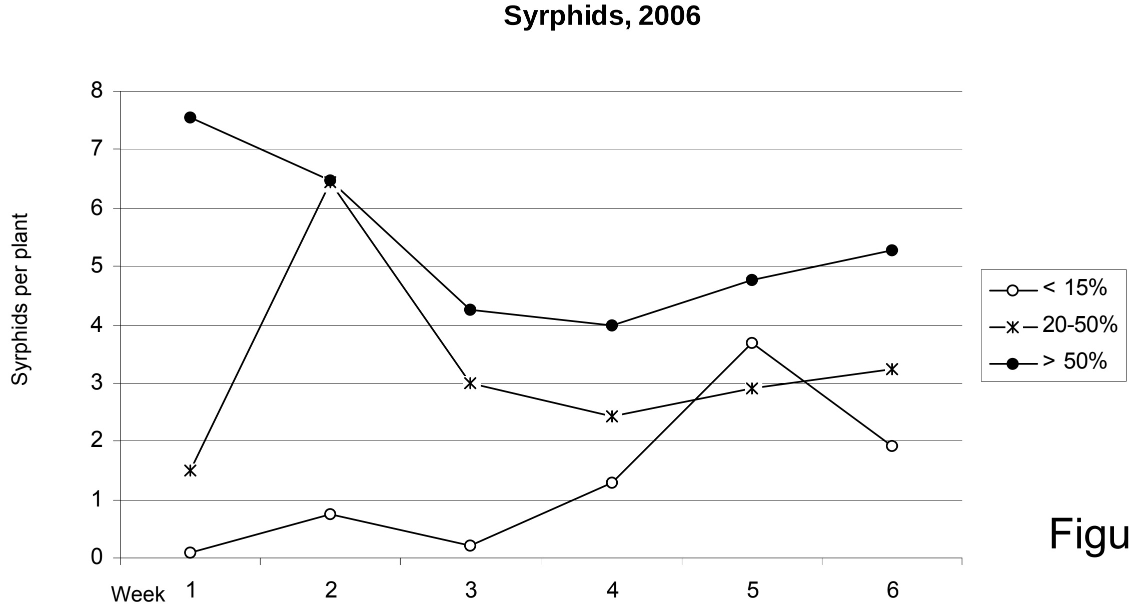

Syrphids, 2006
Syrphids per plant
0
1
2
3
4
5
6
7
8
Week
1
2
3
4
5
6
< 15%
20-50%
> 50%

Figure 6

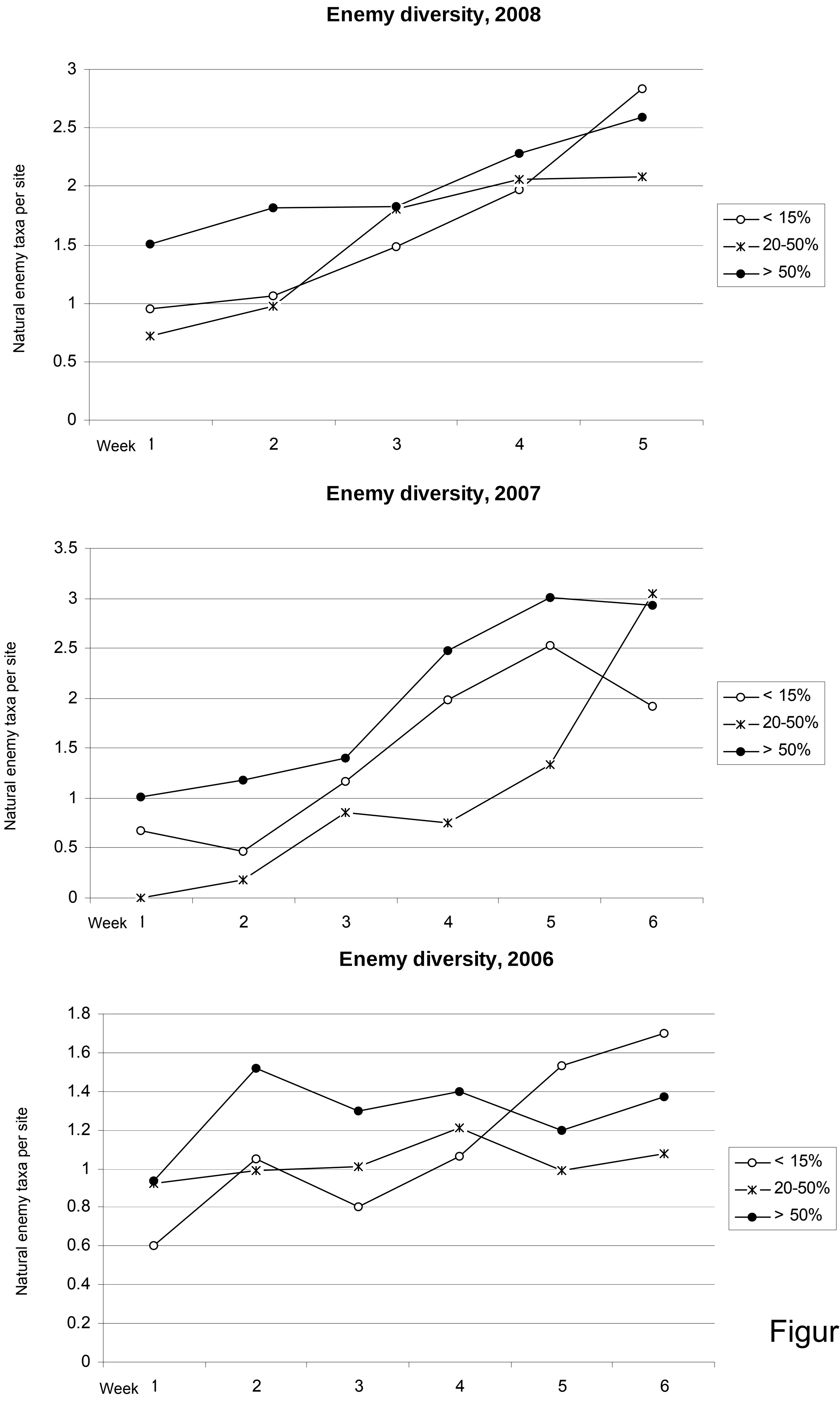
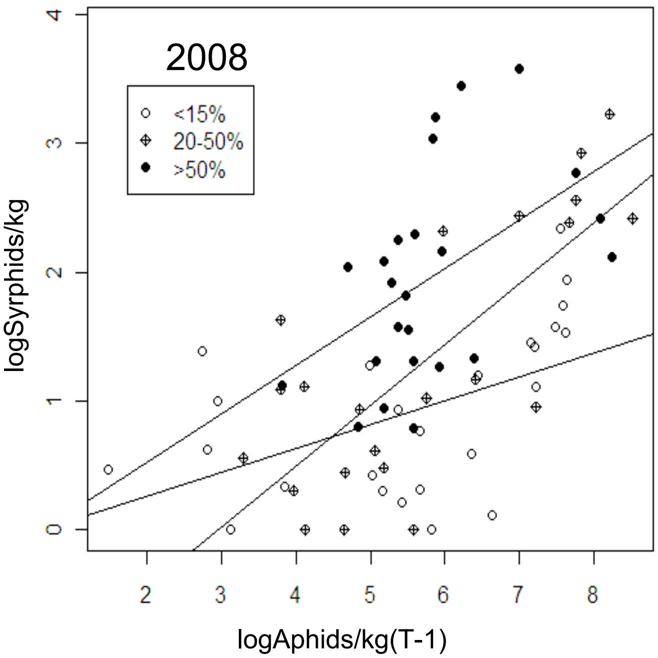
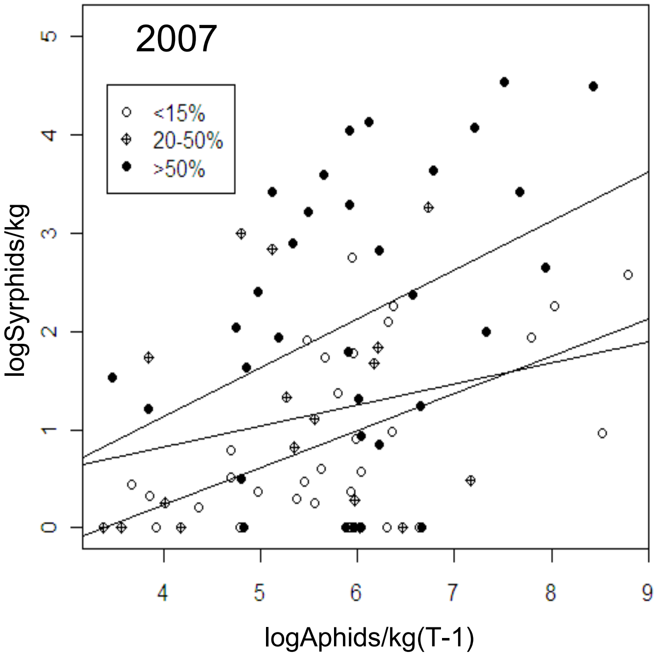

Enemy diversity, 2008
Natural enemy taxa per site
3
2.5
2
1.5
1
0.5
0
Week
1
2
3
4
5
< 15%
20-50%
> 50%
Enemy diversity, 2007
Natural enemy taxa per site
3.5
3
2.5
2
1.5
1
0.5
0
Week
1
2
3
4
5
6
< 15%
20-50%
> 50%
Enemy diversity, 2006
Natural enemy taxa per site
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Week
1
2
3
4
5
6
< 15%
20-50%
> 50%

Figure 7


2008
<15%
20-50%
>50%
logSyrphids/kg
0
1
2
3
4
2
3
4
5
6
7
8
logAphids/kg(T-1)


2007
<15%
20-50%
>50%
logSyrphids/kg
0
1
2
3
4
5
4
5
6
7
8
9
logAphids/kg(T-1)

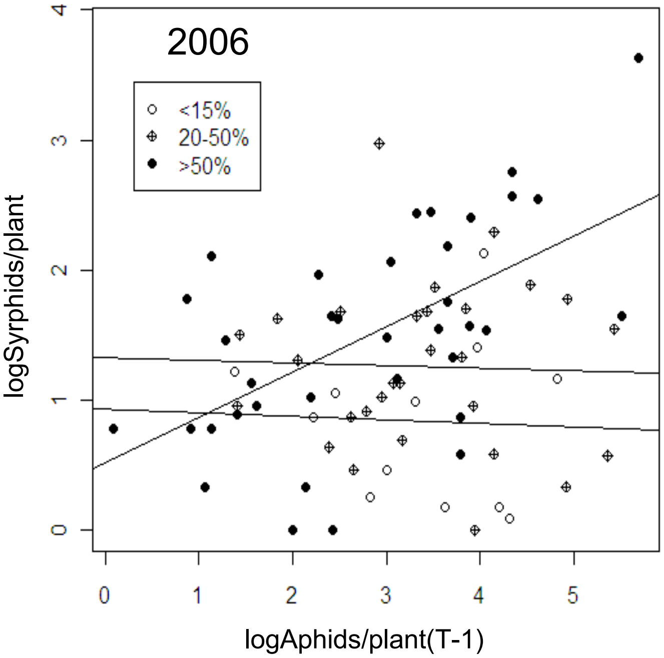

2006
<15%
20-50%
>50%
logSyrphids/plant
0
1
2
3
4
0
1
2
3
4
5
logAphids/plant(T-1)

Figure 8

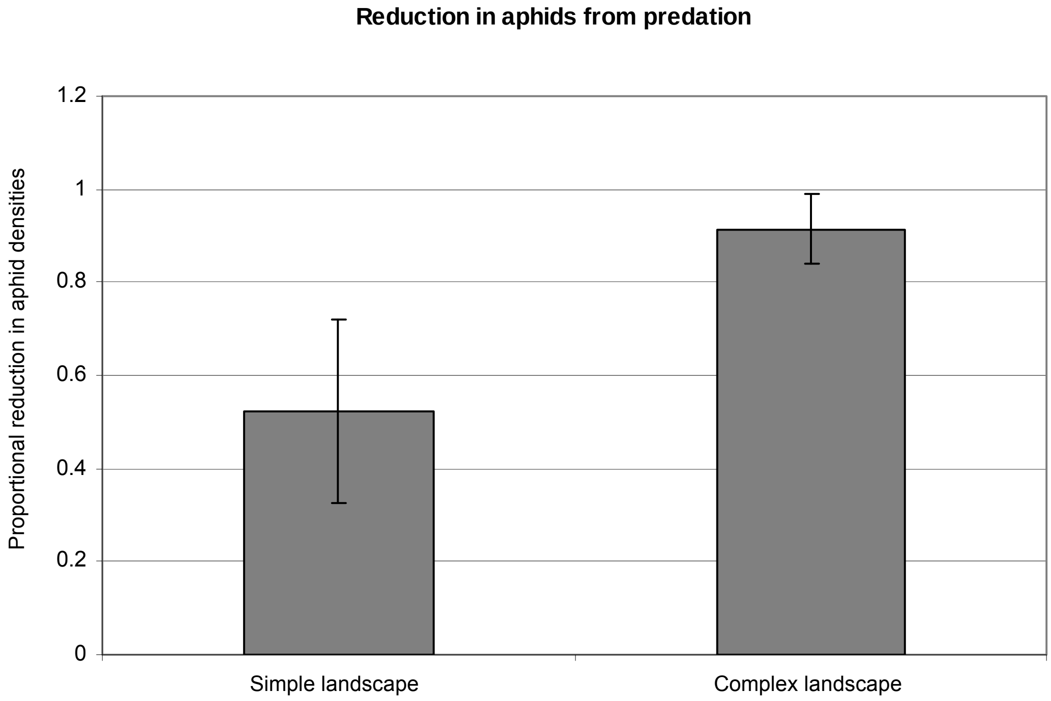


Figure 9a

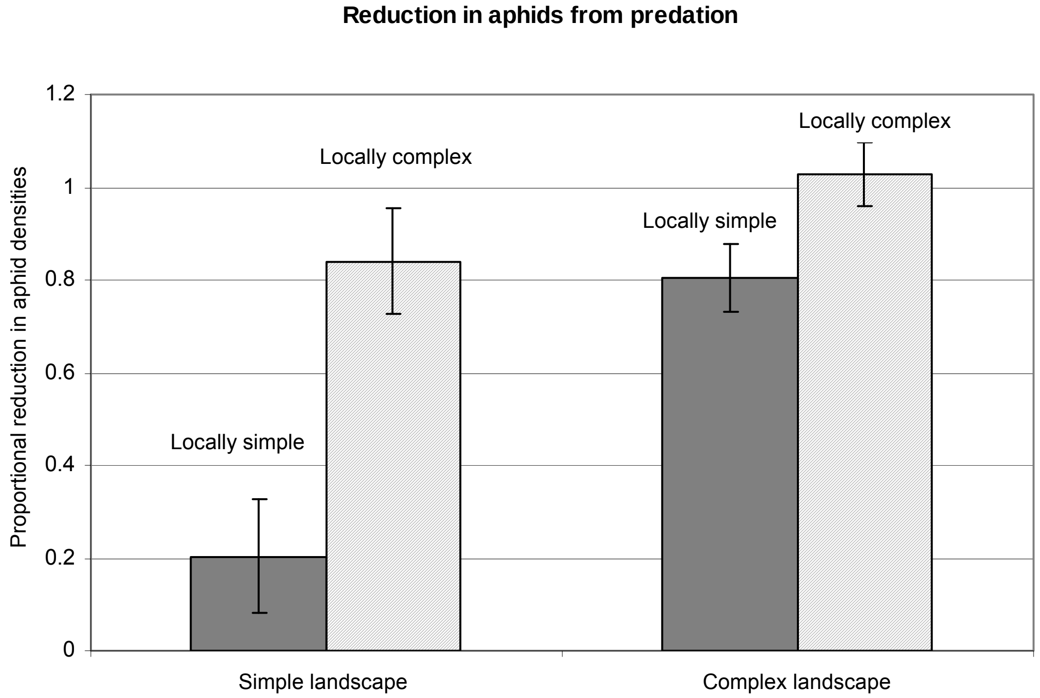


Figure 9b

Figure 10a

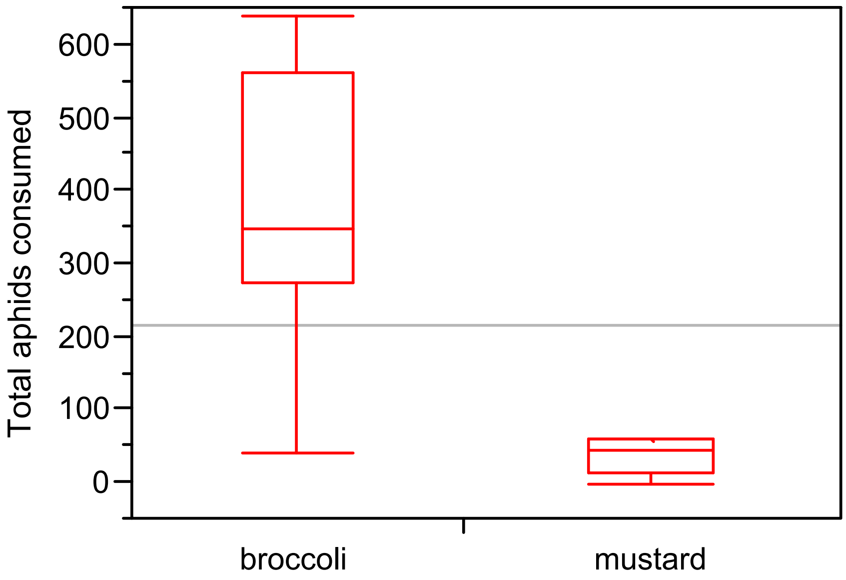


Figure 10b

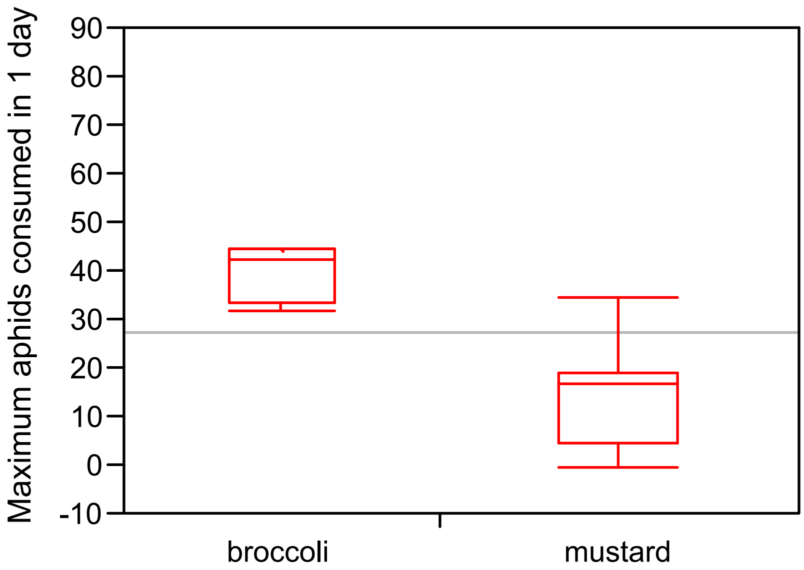


Figure 10c

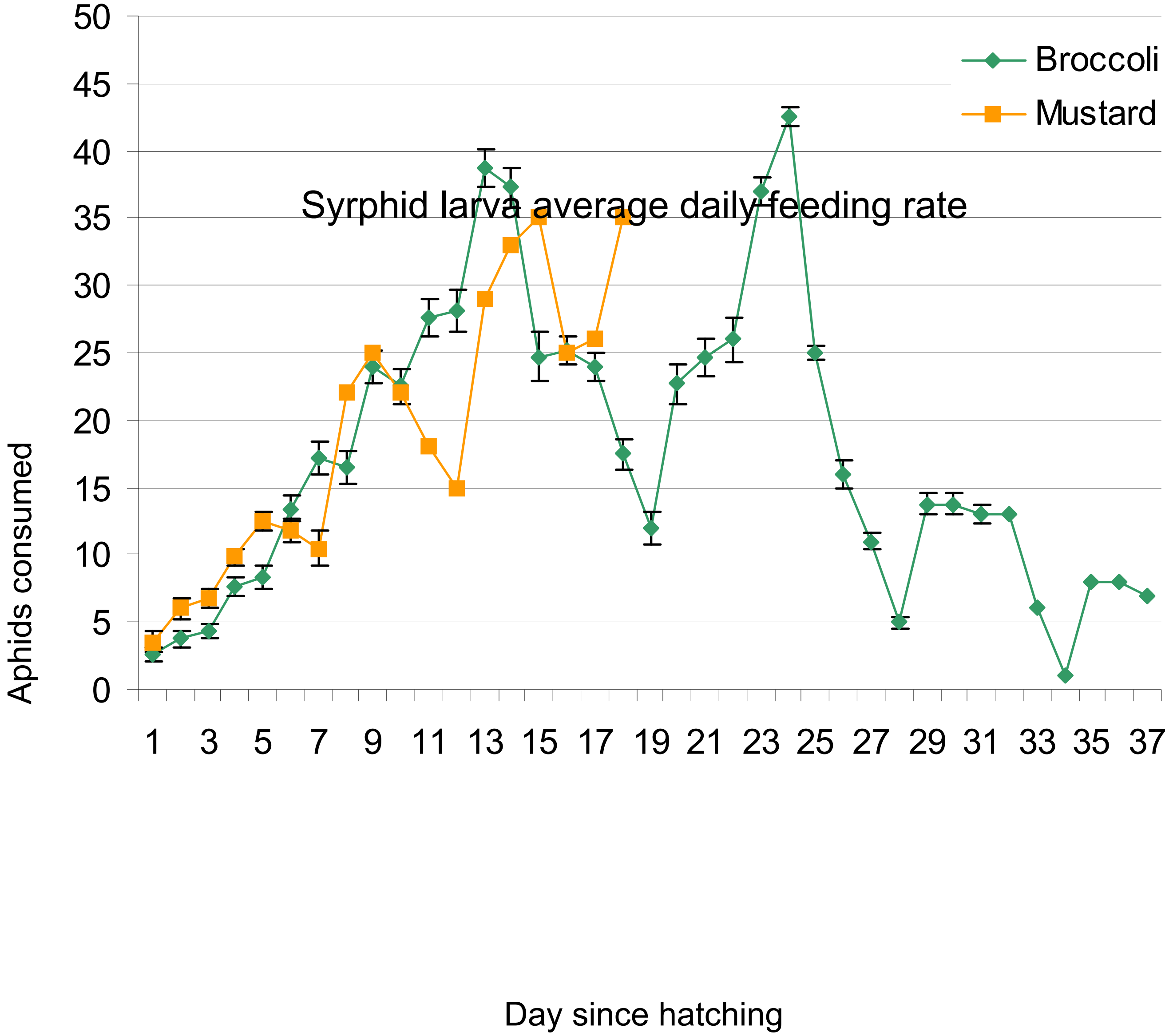

Syrphid larva average daily feeding rate
Broccoli
Mustard
Aphids consumed
0
5
10
15
20
25
30
35
40
45
50
Day since hatching
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37

Figure 11