

EXPLORING THE RELATIONSHIP AMONG PREDATOR DIVERSITY, INTRAGUILD PREDATION, AND EFFECTIVE BIOLOGICAL CONTROL

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ABSTRACT

In conservation biological control, we seek to make agricultural systems more hospitable to natural enemies, in an attempt to increase enemy abundance and diversity. However, it is unclear whether the effectiveness of biological control actually increases with growing natural enemy diversity, in communities including many species of generalist predators. Studies have shown that suppression of herbivores may be either enhanced or disrupted by adding predator species to a community, but these studies do not distinguish between the effects of predator diversity and the effects of predator abundance, identity, and composition. Here, we first demonstrate that a diverse community of natural enemies, dominated by generalist predators, attacks the green peach aphid, *Myzus persicae*, in potato fields in Washington State. Second, in a large-scale field experiment, we experimentally isolate the effect of predator diversity on aphid biological control. We show that increasing predator diversity does not affect prey exploitation; overall there is no strong, net complementarity or interference among predators that alters the strength of aphid suppression. However, our experiment revealed strong effects of predator species identity, because predators varied dramatically in their per capita consumption rates. Because of these strong species identity effects, green peach aphid biological control will improve with growing predator diversity, because particularly effective aphid predators will be more likely to be included within diverse communities. However, our results do not suggest any benefits to biological control of natural enemy diversity *per se*.

INTRODUCTION

Agricultural systems frequently display explosive herbivore outbreaks, while less-disturbed natural communities rarely do. This has led to the suggestion by agroecologists that restoring some elements of biodiversity to agricultural systems may improve natural pest control (Pimentel 1961). However, much recent work in the predator ecology literature suggests that increasing natural enemy diversity increases the risk of adding intraguild predators, such that herbivore suppression might actually decline as predator diversity increases (Rosenheim *et al.* 1993; Snyder and Ives 2001; Snyder and Wise 2001). But few experimental studies have

explicitly examined the relationship between predator diversity and herbivore suppression, in part due to the lack of logistically manageable experimental designs for examining interactions within complex (> 2 predator species) natural enemy communities (but see Finke and Denno 2004).

The growing body of biodiversity-ecosystem function (“BEF”) literature provides experimental approaches that may be useful to predator ecologists (Ives *et al.* 2005). BEF studies typically have demonstrated that ecosystem function, for example, net productivity for plant communities, improves as species diversity increases (Tilman *et al.* 1996; 1997). However, interactions among multiple trophic levels have almost never been considered in the BEF literature (Duffy 2002; Ives *et al.* 2005; Wilby and Thomas 2002). BEF studies share design traits that are unfamiliar to most predator ecologists: treatment levels are the number of species present, with species drawn from a predetermined pool of possible species, and substitutive rather than additive designs are used, so that the total predator densities are constant across diversity treatments (Ives *et al.* 2005).

We have been studying the community of natural enemies attacking the green peach aphid (*Myzus persicae*) in Washington State potato (*Solanum tuberosum*) fields. Our presentation is in two parts. First, we discuss a compilation of taxonomic surveys within potato fields in Washington, demonstrating this crop’s high natural enemy species diversity. Second, we summarize the results of a large-scale field experiment wherein we experimentally constructed natural enemy communities that varied in their natural enemy diversity, and compared the impacts of these communities on green peach aphid.

MATERIALS AND METHODS

DIVERSITY OF NATURAL ENEMIES IN WASHINGTON POTATO FIELDS

In the northwestern United States, insect pests of potatoes have traditionally been controlled using applications of broad-spectrum insecticides (Ruffle and Miller 2003). However, the specter of loss of these chemicals to changes in federal regulations has led some conventional growers to experiment with newer selective pesticides, and organic potato production is growing rapidly in the region. In the 2001-2003 growing seasons we intensively sampled the arthropods in 15 production potato fields under three pest management regimes: conventional fields treated with broad-spectrum pesticides (Hard), conventional fields treated with selective pesticides (Soft), and certified organic fields (Organic) (Koss *et al.* 2005). All fields were within the Columbia Basin of Washington State, a desert region where crops are typically grown under center-pivot irrigation. We sampled arthropods using three techniques: D-vac suction sampling, pitfall trapping, and visual searching (Koss *et al.* 2005).

EXPERIMENTAL MANIPULATION OF PREDATOR BIODIVERSITY

We have conducted a series of experiments wherein we adopted, and somewhat modified, a BEF experimental approach to examine the role of natural enemy species diversity in modifying the control of the green peach aphid (Straub and Snyder, in review). Here, we use one of these experiments to demonstrate our experimental approach and representative results.

In a large-scale field experiment, we experimentally created communities of natural enemies that varied in diversity (either 1 or 3 natural enemy species present), while keeping total predator density constant, and compared the abilities of these communities to control aphids. Our experimental arenas were large, 2m x 2m x 2m field cages, in the field enclosing 4 large potato plants. Cages were first de-faunated using a D-vac suction sampler followed by extensive hand-removal, after which aphids and then predators (according to diversity treatments as described below) were re-added; we then followed the impact of these predator manipulations on aphid population dynamics through time (Straub and Snyder, in review).

In this experiment our species pool included the following five taxa: the predatory bugs *Nabis* spp. and *Geocoris* spp. bug, *Coccinella* and *Harpalus* spp. beetles, and the spider *Misumenops lepidus*. The diversity of taxa (called species here for simplicity) in this predator community has the potential to enhance or disrupt green peach aphid biological control. The considerable variation in foraging behavior among these predators could lead to complementary resource-use and thus a positive relationship between predator diversity and aphid suppression (Ives *et al.* 2005; Wilby and Thomas 2002). However, intraguild predation is also common among these taxa (Brodeur and Rosenheim 2001; Raymond 2000; Snyder and Wise 2001). Such intraguild predation has the potential to lead to a negative relationship between predator diversity and aphid suppression (Finke and Denno 2004; Polis *et al.* 1989; Rosenheim *et al.* 1995). Thus, we had no *a priori* expectations regarding the value of predator diversity in this system. Each of these natural enemy species was present in monoculture, each replicated four times, together comprising the Low Diversity treatment. The High Diversity treatment included 3 predator species, with each of the ten unique combinations of 3 taxa from the pool of 5 replicated once. Thus, our experiment was designed to minimize any influence of species identity, and to isolate any influence of predator species diversity *per se* upon aphid control (Ives *et al.* 2005; Straub and Snyder in review). Ten No Predator control cages were also included, for a total of 40 cages across the experiment. Aphid densities were recorded at 0, 5, and 10 days following predator release.

RESULTS

DIVERSITY OF NATURAL ENEMIES IN WASHINGTON POTATO FIELDS

Geocoris spp. and *Nabis* spp. bugs, and web building tetragnathid and linyphiid spiders, were the most abundant predators in plant foliage, and ground beetles and linyphiid spiders dominated the community on the ground (Table 1). At least 3 parasitoids were common (Table 1). Determining the total number of species that exist in highly disturbed systems like potato fields is difficult. Many species occurring in these fields are immigrants that move in from surrounding vegetation (Wissinger 1997). Rather than attempting to compile and compare complete species lists for fields under each management regime, we took the approach of comparing predator biodiversity using functional groups of taxonomically related species to examine one component of biodiversity, equitability, in our field samples. Overall, equitability scores did not consistently differ between fields receiving hard or soft pesticides, or those under organic management ($P > 0.5$). However, there was a great deal of variability between individual fields (Fig. 1). Some fields had fairly even species distributions, while others were strongly biased towards certain taxa.

Table 1. Common natural enemy taxon groups in Washington potato fields. Data are presented as overall relative abundance of predators, pooling fields across Soft, Hard and Organic management regimes.

Taxon	Common Name	%*	Notes	Functional Group?
In D-vac samples of the foliage (data from Koss 2003)				
<i>Geocoris</i> spp.	Big-eyed bugs	44	<i>Geocoris</i> spp. are active hunters with good vision. They are primarily insectivores, but also do some plant feeding. Adults ca. 5 mm in length.	Foliar Active
<i>Nabis</i> spp.	Damsel bugs	7	<i>Nabis</i> spp. are also active hunters in the foliage, that like <i>Geocoris</i> will do some plant feeding. Adults can be over 1 cm in length.	Foliar Active
Linyphiidae	Sheet web spiders	20	These are tiny spiders (<5mm in length) that build webs to trap prey on the soil surface and lower in the plant canopy.	Trapping
Tetragnathidae	Long-jawed spiders	11	Larger (> 1 cm adult length) spiders that use webs, constructed in the foliage, to capture prey.	Trapping
Other	NA	Each <5	Predatory flies; Orius bugs; lacewings; coccinellid, staphylinid, and carabid beetles; mantids; other spiders. None > 5% of the total.	
In pitfall trap samples (data from Koss 2003)				
<i>Bembidion</i> spp.	Sm. ground beetle	38.5	<i>Bembidion</i> spp. are smaller ground beetles (< 1 cm adult length) active hunters, often diurnal, and sometimes observed in plant foliage	Ground Active
<i>Harpalus fraternus</i>	Lg. ground beetle	16.0	<i>H. fraternus</i> is a larger ground beetle (> 1.5 cm adult length), and active hunter that is usually nocturnal. Less frequently in foliage?	Ground Active
Linyphiidae	Sheet webspiders	13.1	see above	Trapping
Other	NA	32.4	Other carabid spp., staphylinid beetles; other spiders. No single taxon made up greater than 5% of the total.	
In collections of parasitoids emerging from field-collected <i>M. persicae</i> (Data from Pike 2002)				
<i>Aphidius matricariae</i>	none	61.3	Solitary koinobiont, attacks nymph (pref. 3rd instar), emerges from adult or last instar nymph host	Parasitoid
<i>A. ervi</i>	none	15.3	"	Parasitoid
<i>Diaeretiella rapae</i>	none	12.7	"	Parasitoid
Other parasitoids	NA	10.7	A diverse group of other parasitoids; no single taxon > 5% of the total.	Parasitoid

* percentages are proportion of total predator community that taxon represents, across treatments and fields.

EXPERIMENTAL MANIPULATION OF PREDATOR BIODIVERSITY

We measured predator diversity and abundance at the end of the experiment and found that it had changed little. The High diversity treatment remained more species-rich and more diverse than the Low diversity treatment (richness, $t_{28} = 2.544$, $P < 0.05$; Simpson's diversity index, $t_{28} = 2.735$, $P < 0.05$; Straub and Snyder, in review). There was no difference in predator abundance between diversity treatments ($t_{28} = 0.886$, $P > 0.10$), suggesting that overall rates of predator interference were not different under Low versus High predator diversity (Straub and Snyder, in review). There was no evidence that predator diversity impacted aphid suppression: aphid densities were consistently lower in treatments including predators, compared to No Predator controls [Predator addition (High diversity + Low diversity) vs. Control; Exp 1: $F_{1,38} = 10.442$, $P < 0.01$], but aphid densities were indistinguishable in Low and High diversity cages (treatment x time Wilks' lambda = 0.846, $F_{2,27} = 2.454$, $P > 0.10$; diversity $F_{1,28} = 1.542$, $P > 0.10$) (Straub and Snyder, in review). We then asked if species identity might be a better predictor of herbivore suppression. Using Paine's interaction strength index (Paine 1992) to quantify the per-capita impact of predators, we found that species identity had a strong effect on herbivore suppression ($F_{4,15} = 7.028$, $P < 0.01$), with *Coccinella* beetles provided stronger, and thomisid spiders weaker, suppression than in the High diversity treatment (Straub and Snyder, in review).

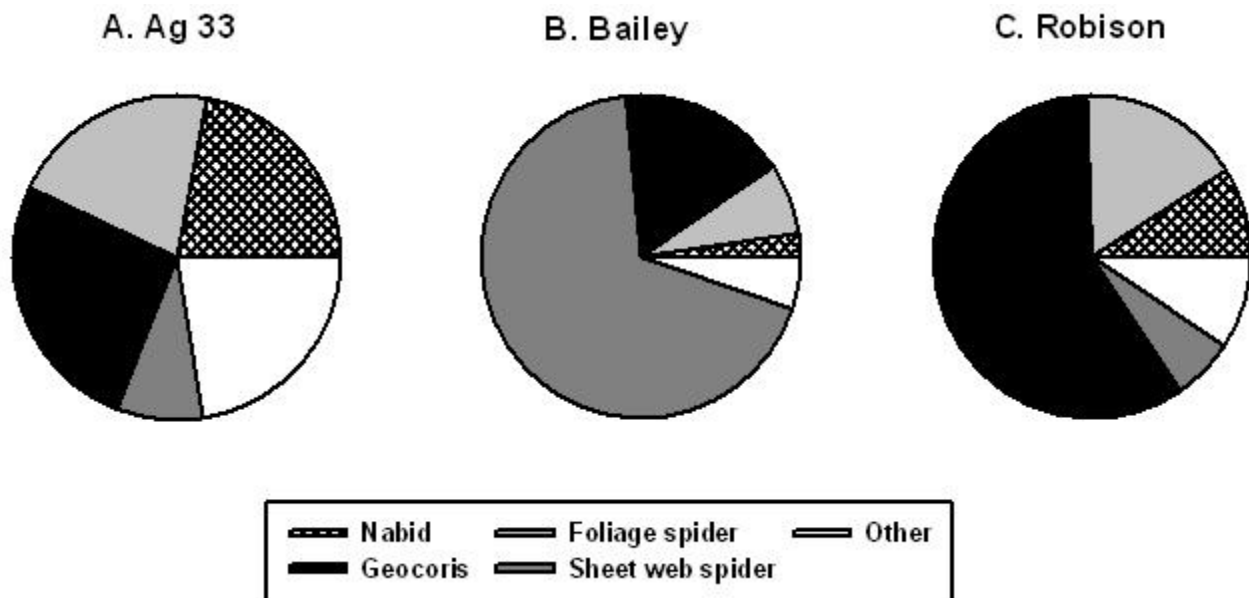


Figure 1. Predator community makeup in three fields in 2001. A) Ag 33 was a Hard field; B) Bailey was a Soft field; and C) Robison was a Hard field. These fields represent the three equitability patterns we saw in the field. Ag 33 has a high equitability score, because the major taxa are similar in abundance. Bailey and Robison have uneven taxa abundances, yielding low equitability scores. However, while their equitability scores are similar, species composition is not – Bailey is dominated by the Trapping functional group, while Robison is dominated by Foliar Active predators.

DISCUSSION

The community of natural enemies attacking green peach aphid locally is diverse, including many species of generalist (and thus likely intraguild) predators. Our predator community includes >20 common species. Therefore, functional diversity of the type necessary for species complementarity, and thus a positive relationship between natural enemy diversity and more complete resource exploitation (Naeem and Wright 2003), likely is present in this community. However, despite our attempts to include representative functional diversity within our field experiment, we found that varying predator diversity *per se* had no effect on the strength of aphid control. It is perhaps surprising that there was no evidence for species complementarity leading to an increase in the strength of herbivore suppression. Our predator species were chosen to span a range of hunting strategies, including active hunters in the foliage, active hunters on the ground, and sit-and-wait hunters in the foliage. Also, we intentionally included one pair of taxa, *Coccinella* and *Harpalus*, which constitute one of the best-documented cases of predator facilitation in a terrestrial system (Losey and Denno 1998). Nonetheless, we recorded no increase in the efficiency of aphid exploitation by more species-diverse natural enemy communities.

Intraguild predation also appeared to be a weak force in our experiment. This result appears in stark contrast to experiments that have shown strong disruptive effects of intraguild predation on herbivore suppression (e.g., Finke and Denno 2004; Rosenheim *et al.* 1993; Snyder and Ives 2001). The lack of intraguild predation in this study is unlikely to be entirely due to an inherent reticence towards intraguild predation within our communities, as many of the included taxa have been shown to feed on one another. For example, *Nabis* and *Geocoris* feed on one another (Raymond 2000), *Harpalus* eats *Nabis* (Snyder and Wise 2001), and most of the predators feed on parasitoids (Brodeur and Rosenheim 2000). One interesting explanation for the difference between the results of this and other studies is that we used a substitutive, rather than an additive, experimental design. Additive designs have often shown strong, disruptive intraguild predation among species (Finke and Denno 2004; Rosenheim *et al.* 1993; Snyder and Ives 2001). However, compared with substitutive designs, additive designs may deflate intraspecific interference and inflate interspecific interference. This is because, in additive designs, predator encounter rates and competition for prey will be higher in treatments including multiple predator species because these treatments also include higher overall predator densities. Regardless, our results suggest that greater predator diversity does not generally weaken pest suppression, as might be surmised from the numerous studies emphasizing the negative effects of predator interference among species (e.g., those reviewed in Polis *et al.* 1989; Rosenheim *et al.* 1995). This is good news given that sustainable agricultural practices such as organic farming often lead to greater on-farm diversity (Hole *et al.* 2005).

The finding that predator identity is a better determinant of pest suppression than predator diversity also has implications for biological control. It implies that, for the biological control of any one pest species, conservation strategies that target particularly effective predator species will be more effective than those targeting predator diversity more broadly. This result supports the common-sense view that conservation biological control practitioners should strive to identify and manage for “the right kind of diversity”, rather than managing for greater biodiversity itself (Landis *et al.* 2000).

In summary, our results suggest that predator diversity *per se* has little effect on the strength of aphid suppression. This result is in contrast with BEF work at other trophic levels, which has consistently revealed a positive relationship between rising consumer biodiversity and the efficiency of resource utilization (Cardinale *et al.* 2002; Naeem and Wright 2003; Tilman *et al.* 2001). Thus, pest suppression may be less sensitive than other ecosystem services to biodiversity loss, provided that key predator species are conserved.

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REFERENCES

- Brodeur, J., and Rosenheim, J. A. 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* **97**, 93-108.
- Cardinale, B. J., Palmer, M. A., and Collins, S. L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**, 426-429.
- Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**, 201-219.
- 478 Finke, D. L., and Denno, R. F. 2004. Predator diversity dampens trophic cascades. *Nature* **429**, 407-410.
- Hole, D. G., Perkins, A. J., Wilson, J. D., Alexander, I. H., Grice, P. V., and Evans, A. D. 2005. Does organic farming benefit biodiversity? *Biological Conservation* **122**, 113-130.
- Ives, A. R., Cardinale, B. J., and Snyder, W. E. 2005. A synthesis of sub-disciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters* **8**, 102-116.
- Koss, A. M., Jensen, A. S., Schreiber, A., Pike, K. S., and Snyder, W. E. 2005. A comparison of predator communities in conventional potato fields treated with broad-spectrum or selective pesticides, and organic fields. *Environmental Entomology* **34**, 87-95.
- Landis, D. A., Wratten, S. D., and Gurr, G. M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* **45**, 175-201.
- Losey, J. E., and Denno, R. F. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* **79**, 2143-2152.
- Naeem, S., and Wright, J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**, 567-579.
- Paine, R. T. 1992. Food-web analysis through field measurements of per-capita interaction strength. *Nature* **355**, 73-75.

- Pike, K. S. 2002. Green Peach Aphid and Aphid-Parasite Regional Assessment and Management. 2002 Progress Reports, Washington State Potato Commission, Moses Lake, WA. Pp.173-181.
- Pimentel, D. 1961. Species diversity and insect population outbreaks. *Annals of the Entomological Society of America* **54**, 76-86.
- Polis, G. A., Myers, C. A., and Holt, R. D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**, 297-330.
- Raymond, B. 2000. "Cannibalism and Intraguild Predation Involving Three Predatory Heteroptera, *Nabis roseipennis*, *Geocoris punctipes* and *Orius insidiosus*." Ph.D. Dissertation, University of Kentucky, Lexington, KY, USA.
- Rosenheim, J. A., Wilhoit, L. R., and Armer, C. A. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* **96**, 439-449.
- Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Marois, J. J., and Jaffee, B. A. 1995. Intraguild predation among biological-control agents: theory and practice. *Biological Control* **5**, 303-335.
- Ruffle, R., and Miller, J. 2003. Digging for Alternatives: An Analysis of Potato Pest Management Research at Two Northwest Land Grant Universities. Northwest Coalition for Alternatives to Pesticides, Eugene, OR.
- Sih, A., Englund, G., and Wooster, D. 1998. Emergent impacts of multiple predators on multiple prey. *Trends in Ecology and Evolution* **13**, 350-355.
- Snyder, W. E., and Ives, A. R. 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* **82**, 705-716.
- Snyder, W. E., and Wise, D. H. 2001. Contrasting trophic cascades generated by a community of generalist predators. *Ecology* **82**, 1571-1583.
- Straub, C. S., and Snyder, W. E. In review. Species identity dominates the relationship between predator diversity and herbivore suppression. *Ecology*.
- Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718-720.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300-1302.
- Wilby, A., and Thomas, M. B. 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters* **5**, 353-360.
- Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in an annual cropping system. *Biological Control* **10**, 4-15.