MECHANISMS DRIVING INCREASED PREY CONSUMPTION WITH INCREASING

PREDATOR DIVERSITY

By

GRETCHEN BETH SNYDER

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of
GRETCHEN BETH SNYDER find it satisfactory and recommend that it be accepted.

_____
William E. Snyder, Ph.D., Chair

_____
Stephen L. Clement, Ph.D.

_____
Sanford Eigenbrode, Ph.D.

_____
Jeb P. Owen, Ph.D.

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Abstract

by Gretchen Beth Snyder, Ph.D.

Washington State University

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Chair: William E Snyder

Theory predicts that greater prey diversity will both foster the emergence of complementary predator feeding patterns and weaken any negative effects of intraguild predation. Thus, a positive relationship between predator diversity and improved prey suppression might be realized when several prey species are present, if a diversified prey base allows complementarity among predators to be realized. In two 2005 field cages experiments in Othello WA, I examined the effects of including multiple prey species on predator diversity by simultaneously manipulating presence or absence of multiple prey (one or two species) and predator diversity (monoculture or polyculture). We found the strength of aphid suppression always increased with greater predator biodiversity, but this effect was independent of prey species diversity or identity. This suggests that the benefits of predator diversity for prey suppression were mediated by interactions within the predator community, such that a diverse resource base was not necessary to yield a positive relationship between predator biodiversity and effective herbivore suppression.

The strength of herbivore suppression often improves with greater predator biodiversity,

but controversy remains about the mechanism(s) underlying such results. Positive diversity effects might result from partitioning of the prey resource, with different predator species attacking different subsets of the prey population, a release from intra-specific competition, or facilitation. In two 2007 field cage experiments I manipulated diversity, and also density, among a community of predators, and measured the impact of these manipulations on densities of aphid prey. Predator polycultures exerted the strongest aphid suppression, and only among polycultures did aphid suppression increase across all predator density levels. In addition, we found that multi-predator effects were approximately additive, consistent with a release from intra-specific competition in high diversity predator treatments. Taken together, our results provide compelling empirical evidence that, in this system, weaker interspecific than intraspecific competition underlay stronger prey suppression with greater predator biodiversity

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for my daughters Gabriella and Madison Garcia

CHAPTER ONE

GENERAL INTRODUCTION

Biodiversity and Ecosystem Function studies brief history

Concerns regarding the unprecedented rate of species extinctions experienced worldwide

(Ehrlich 1988, Wilson 1988, Naeem et al. 1995, Stork 1997, Tilman et al. 1997, Chapin III et al.

1998, Pimm and Raven 2000), coupled with projections of future extinctions due to continued

habitat loss/climate change (Chapin et al. 1995, Chapin et al. 1996, Hooper and Vitousek 1998,

Pimm and Raven 2000), and the consequences of these extinctions on how ecosystems function

(Hector et al. 1999, Sala 2000, Loreau et al. 2002, Naeem 2002, Jonnson 2006) has created an

area of research known as Biodiversity and Ecosystem Functioning (BEF). BEF studies seek to

answer the question: does the loss of biological diversity affect how ecosystems function

(Vitousek and Hooper 1993, UNEP 1995, Mooney and al. 1996, Loreau et al. 2002)? Though

research directed specifically at BEF can be traced back only to the early 1990's, its theoretical

and empirical roots have a much longer and richer history.

Theoretical beginnings of BEF studies

Darwin and Wallace (1858) suggested that diversity and productivity are positively linked when

he noted that in agricultural fields, plants grown in concert with other crops out-produced those

grown singly. Though prescient this suggestion was without proposed mechanisms. The first

theoretical papers that deal specifically with diversity and ecosystem function were written by

Elton (1927), Odum (1953), and MacArthur (1955), all of whom supported the idea that habitat

complexity (diversity) fostered ecosystem stability as defined by either reduction of population variation or decreased susceptibility to invasion. Odum (1953) and MacArthur (1955) each proposed that dampening oscillations of constituent species populations led to community stability. Stability would be more likely under high diversity because of the greater number of alternative paths for energy flow through the food web. Elton (1927) proposed that more diverse communities would less likely be dominated by an invasive species because greater diversity would present greater competition for resources, making colonization more difficult for the invading species (Elton 1927).

For nearly twenty years after these early ecology papers, the idea that complexity and stability were positively correlated was the broadly accepted paradigm. Until the paradigm was challenged using by Gardner and Ashby (1970) using a mathematical argument based on comparing matrices of simulated data drawn from random that suggested stability of a system increased with increasing connectedness (diversity) but only up to a critical point, beyond which the system became unstable. Other modelers followed suit and found that stability decreased as diversity increased (May 1973, Levins 1974). Finally, Goodman (1975) published a review paper on the theory of diversity-stability relationships, concluding that theory was not supported by observations of natural systems. Goodman cited a study by Smith (1970) as an example which stated that ecosystems with relatively high levels of diversity were subject to population fluctuations just as large as those in more species-poor communities. Goodman also stated that tropical rain forests (noted for their high diversity) were particularly susceptible to anthropogenic perturbations (Gómez-Pompa et al. 1972, Bretsky et al. 1973). In addition, empirical studies and computer simulations rarely support a diversity-stability relationship (Goodman 1975). Goodman came to the conclusion that there was no clear relationship between diversity and ecosystem

stability. The mathematical rigor of May's models (1973), coupled with ambiguities in how stability and diversity were defined, and a lack of evidence that the diversity-stability relationship existed in natural systems, led to an almost complete abandonment of the idea (Kinzig et al. 2001). This new paradigm went virtually unchallenged throughout the 1970's and 1980's (but see King and Pimm 1983, Pimm 1984).

Empirical beginnings of BEF studies

The first empirical studies that addressed a relationship between increasing diversity and ecosystem function were intercropping studies (e.g. Ahlgren and Aamodt 1939, Aberg et al. 1943), and studies designed to test the diversity-stability theory (Hurd et al. 1971). Trenath (1974) reviewed 344 mixture studies and found that overall primary production within polycultures was usually above the mean production of the component species grown in monoculture (Trenbeth 1974). Likewise, McNaughton (1977) reviewed two earlier studies, along with data from a successional grassland study, and concluded that stability increased with stability in all three (but see Goodman [1975] above). Empirical studies seeking to test the diversity-stability hypothesis suffered the same fate as theoretical studies, and fell out of favor because of how stability and diversity were defined, as well as a lack of evidence that the diversity-stability relationship existed in natural systems. Though some researchers continued to study the role of biodiversity (e.g. King and Pimm 1983, Pimm 1984), it was not until a meeting in Mitzwitz, Germany in the early 1990's that BEF studies began again in earnest (Loreau 1998a).

Scientific Committee on the Problems of the Environment (SCOPE)

In 1991, an international group scientists gathered in Mitwitz, Germany, to try to unite the disparate theories of population, community, and ecosystem ecology in regards to BEF research. This group, named the Scientific Committee on the Problems of the Environment (SCOPE), addressed a growing concern among the pubic and scientific community about environmental changes and the consequences of those changes on earth's ecosystems (UNEP 1995, Hector et al. 1999). The impetus for SCOPE was a concern that ecosystem ecologists were studying global changes of biogeochemical processes and energy cycles with an overreaching assumption that the earth's organisms were a constant. Rather, SCOPE noted, these systems are dynamic. As dynamic systems they are capable of undergoing changes concomitant with changes in biogeochemical/energy cycles. In addition these changes are potentially mutually causally linked (Loreau 1998a). Of specific concern was that biodiversity, within and among species worldwide, was decreasing (Ehrlich 1988, Wilson 1988, Naeem et al. 1995, Stork 1997, Chapin III et al. 1998, Loreau 1998a, Pimm and Raven 2000). Though community ecologists recognize that key species could have widespread effects on ecosystem functioning (Paine 1969, 1980, Power et al. 1996), there was little empirical evidence for the consequences of losses of biodiversity for biogeochemical and energy cycles. After SCOPE, many international committees were created to address the consequences of biodiversity loss to ecosystem function and services (e.g. Global Biodiversity Assessment [GBA], Global Change and Terrestrial Ecosystems [GCTE], and DIVERSITAS) More importantly, new direction emerged in Biodiversity and Ecosystem Function.

Early BEF studies

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Some of the first BEF empirical studies were published in Nature (Naeem et al. 1994, Tilman and Downing 1994). In 1988 a severe drought at David Tilman's open field (University of Michigan, KBS) site allowed him to test empirically the diversity-stability hypothesis by directly comparing the resistance and recovery of primary production of low diversity plots (mono-cultures) with plots with increasing levels of diversity. Primary production of plants was increasingly resistant to, and recovered "more fully" from the draught with increasing levels of plant diversity. Tilman and Downing (1994) had a large impact on the scientific community because the experiment was done in an open grassland setting and at a relatively large spatial and temporal scale. It was pivotal to challenging the existing paradigm that increased diversity destabilized ecosystems (Kinzig et al. 2001, Loreau 2002). Though the work published by Naeem et al. (1994) was done in a laboratory setting, it also strongly influenced the direction of BEF studies. Naeem et al. (1994) addressed a different aspect of BEF than did Tillman and Downing (1994) by measuring five ecosystem processes in a multi-trophic system: community respiration, decomposition, nutrient retention, plant productivity, and water retention. Like Tillman and Downing (1994), Naeem et al. (1994) found a positive relationship between biodiversity and efficiency of ecosystem function. The implied dire consequences for the functioning of ecosystems following species loss, in particular the loss of the services they provide humans, inspired many more BEF studies.

As is true with most new areas of science, the two studies afore mentioned studies were met with rigorous debate centered on the following issues: questions regarding the appropriate experimental design; data analysis issues; experimental scale appropriate for addressing these questions; and the general conclusions that could be drawn from these studies (Aarssen 1997, Houston 1997, Wardle 1999). For example, these original studies randomly drew diversity

treatments with replacement from a pool of species. Because of this, high diversity treatments were more likely than low diversity treatments to include species that were particularly effective purveyors of particular ecosystem functions (Aarssen 1997, Houston 1997, Tilman 1997). Thus, increased function at higher levels of diversity might occur not because of diversity *per se*, but rather because of an increased likelihood of including the dominant species at higher diversity levels. This problem was termed the "sampling effect" (Aarssen 1997, Houston 1997, Wardle 1999). In addition, high diversity treatments were more alike than low diversity treatments, which can reduce variability within high diversity treatments (Houston 1997, Wardle 1998, Fukami et al. 2001). Also, empirical studies covered relatively short time scales, which might make intrinsic factors appear to be important, when in reality they could be swamped by extrinsic factors (Grime 1997, Wardle et al. 1997). Indeed, a recent meta analysis found that the strength of a diversity effect increased as investigators controlled for extrinsic factors (i.e. moved from field manipulations to controlled environment greenhouse experiments) in studies where diversity was manipulated (Balvanrea et al. 2006). Still other ecologists questioned the ability of scientists to infer consequences of diversity loss at a global scale based on experiments that are confined to smaller spatial and temporal scales (Carpenter 1996, Bengtsson et al. 2002).

In more recent studies, some of the afore mentioned concerns have been addressed by modifications to experimental design. For example, to lessen the chance of the sampling effect, species deletion treatments, instead of random draws, can be used to assemble high diversity treatments (Fridley 2001, Huston and McBride 2002). In this design, instead of drawing species with replacement from a pool of species, high diversity treatments include combinations of the pool of species with a single species deleted (Fridley 2001). To avoid the sampling effect, every possible combination of species should be included at each level of diversity (Straub and Snyder

2006a). However, as a tradeoff, this increases the number of treatments and limits the number of species that are feasible to include in a study (e.g. Snyder et al. 2005, Straub and Snyder 2006b). In addition, it has been pointed out that when specific species are chosen for high diversity treatments, conclusions should be limited only to the particular group of species and only within the study system rather than making inferences on diversity effects in general (Jonnson 2006). Evidence that no one species dominates ecosystem function in high diversity treatments can also be indirectly found by comparing the average of the component species' performance in mono-culture, to the average performance of polycultures within the context of a substitutive experimental design (Loreau 1998b, Loreau and Hector 2001). Transgressive over-yielding (i.e. no single component species outperforms the poly-culture) is evidence against a diversity effect driven by one species (sampling effect). However for this comparison to be made, all species must be included in monoculture which can also limit the number of species an ecologist can include in a study (Schmid et al. 2008).

Limitations of BEF studies

There are limitations inherent to empirical studies to address the functioning of an entire ecosystem. Both theoretical and empirical BEF studies seek to understand the global consequences of decreased biodiversity. Thus, in its broadest sense, biodiversity is meant to encompass all measures of diversity, including not only species richness, but also the richness and evenness among populations, functional groups, and landscape types (Mooney and al. 1996, Hector et al. 1999, Loreau et al. 2002, Jonnson 2006). Likewise, ecosystem function encompasses not just the productivity of an ecosystem but also nutrient cycling, decomposition, stability, resistance to perturbation, and how all of the aforementioned processes feed back into

biogeochemical cycles (Loreau et al. 2002).While theory is able to address biodiversity effects in general at this global level, the inevitable constraints inherent to empirical research limit the testing of theory at large spatial and temporal scales, and with the number of species needed, to make global conclusions. Due to these constraints, most empirical studies are small scale, conducted for short durations and with a depauperate pool of species as compared with natural systems. Moreover, because species diversity is easily defined and manipulated, a preponderance of studies focuses on species richness, neglecting other components of biodiversity (Balvanrea et al. 2006). For similar pragmatic reasons, primary production is often measured as a surrogate for all of ecosystem function (for a review of BEF studies that measure primary production see Hector et al. [1999]). How then do ecologists progress towards measuring the effects of a loss of diversity on ecosystem functioning, and further on the ecosystem services humans rely on for survival? Perhaps the only way is to conduct diverse manipulative experiments and employ meta-analyses to detect general trends. This can be accomplished by including studies with varying spatial and temporal scales that measure multiple ecosystem function traits and include both single and multiple trophic levels

Determining the current status of BEF studies using reviews/meta-analyses

Five reviews/meta-analyses have been published on BEF studies. I review them in order of publication date below (Hooper 2005, Balvanera et al. 2006, Cardinale et al. 2006a, Dufffy et al. 2007, Stachowicz et al. 2007).

Hooper et al. (2005) made several conclusions. First, they concluded that species functional characteristics strongly influence ecosystem function (i.e. the sampling effect). In order to predict how an ecosystem will function after the loss of species it is just as important to

know what species/functional groups are present in the system is as knowing the number of species. The empirical studies referenced in this review were mostly grassland diversity studies and studies on soil processes. Second, they conclude that the effects of a loss of biodiversity vary in magnitude depending on what ecosystem service is being measured as the response variable, and also on the functional groups and the ecosystem types being considered. With herbaceous plants, plant productivity increases with increasing plant diversity and tends to saturate around 5-10 species (e.g. Tilman et al. 1996, 2001, 2002, Hector et al 1999), but this increase was not always seen with longer living perennials that saturate at one or two species (e.g. Ewel et al. 1991 Haggar and Ewel 1997). Facilitation was most common in unproductive/stressful environments, while complementarity tended to dominate with greater resource availability. Third, Hooper et al. (2005) concluded that in general diversity should be conserved to ensure proper ecosystem function with increasing spatial and temporal variability. The reason for this is that as local habitats loose species a greater pool of possible immigrants is needed at a regional scale to increase the odds that the immigrant species can function similarly to those species lost at the local scale. In addition, temporal changes, such as continued anthropogenic changes to the environment, increase the need for diversity in order to increase the chances of including species/functional groups that can adapt to these changes and still maintain ecosystem function.

Balvanera et al. (2006) concluded that increasing bio-diversity had a positive effect on most of the ecosystem services assessed in their meta-analysis. Biodiversity effects were weaker when manipulations were in fields rather than more controlled environments like greenhouses. The magnitude of the effects of diversity decreased as the number of species (or other diversity components) decreased. The authors of this meta analysis differentiated between the organizational level of the ecosystem properties measured. A population level measure was

defined as, properties recorded for one target species. A community level measure used

information from multispecies assemblages. An ecosystem level measure was defined as one that

measured abiotic ecosystem components (e.g. nutrients, CO_2). Diversity effects were strongest at

the community level, weaker at the ecosystem level and negative at the population level.

Productivity measures declined with increasing distance of trophic links from the trophic level at

which diversity was manipulated (Balvanrea et al. 2006).

In a meta-analysis, Cardinale et al. (2006) found that, on average, a decrease in species

richness leads to less complete depletion of resources used by the focal trophic group, but there

was a trend for the sampling effect to drive diversity effects. That is, the identity of species lost is

important for ecosystem function.

Stachowicz et al. (2007) reviewed the literature of marine systems and reported that

85/123 studies found a general trend for a positive relationship between increased biodiversity

and increased ecosystem function.

Finally, Duffy et al. (2007) determined that, generally speaking, resource use/biomass

increased with increasing diversity for both producers and consumers.

All of the above listed studies found a general trend of an increase in ecosystem function

with increased diversity. It is tempting to accept that the current consensus of BEF studies is that

ecosystem function increases with diversity increases. However, most of the papers included in

these reviews and meta-analyses manipulated diversity at only one or two trophic levels: either

manipulating the diversity of primary producers and then measuring their productivity (e.g.

Tilman 1996, 2001 Hector et al. 2000), or less frequently including primary consumers (e.g.

herbivores) thereby including two trophic levels (Norberg 2000, Cardinale & Palmer 2002). Few

studies include secondary consumers (e.g. predators), which yields three trophic levels

(Cardinale 2003, Aquilino et al. 2005, Wilby et al. 2005, Snyder et al. 2006, Snyder et al. 2008). There is one study, which I review next, that included fourth and fifth trophic levels by including parasitoids and hyperparasitoids. Even though the lines of trophic levels can be blurred by the occurrence of omnivory and intra-guild predation (Polis1991, Strong 1992, Polis and Strong 1996, Snyder and Wise 2001), the concept of distinct trophic levels is useful to differentiate between the levels of organisms manipulated in BEF experiments.

Single and double trophic level bias? in empirical BEF studies

All of the studies reviewed above were dominated by research that included only one or sometimes two trophic levels. Only one section in Hooper et al. (2005) (section II.A.2.[f]) focuses on varying diversity of heterotrophs, and there are only 13 empirical studies cited in this section. In the meta-analysis by Balvanera et al. (2006), there were 446 manipulations of diversity: 319 were of primary producers and only 4 were of the third trophic level (predators). In the Cardinale et al. (2006) meta-analysis there were 58 studies /111 experiments, and of these just 9 studies manipulated predator diversity. Stachowicz et al. (2007) reviewed marine systems. This review contained a greater proportion of two-trophic level systems than the three previous papers: 23 out of the 51 studies reviewed manipulated primary producers (first trophic level), 8 manipulated herbivores (second trophic level), 8 manipulated grazers (second trophic level), 8 suspension and deposit feeders, and only 4 manipulated predators (third trophic level). The review paper by Duffy et al. (2007) is unique among all of the other analyses in that its central focus was the incorporation of trophic complexity into BEF studies. Studies listed were all

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designed to look for intertrophic effects of manipulating diversity at one or more trophic levels. Even so, of the 26 empirical studies mentioned in this review, only 8 independently manipulated diversity of the third trophic level to measure the resulting resource consumption of the previous trophic level. The fact that only 30% of empirical studies designed to include multitrophic effects include identifiable predator-prey interactions, emphasizes the need for more such experiments in a BEF context. It is important to note that 6 more studies in this section included a third trophic level, but for various reasons did not test diversity of that level *per se* on resulting resource consumption (see next section for more details).

Thus, this positive trend of increasing diversity on increased resource consumption is not clear in complex multi-trophic food webs, such as those that include predator-prey interactions (Bruno and Cardinale 2008).

Role of predator diversity in BEF studies

Empirical studies that manipulate predator diversity are rare. Of the 13 empirical studies in Hooper et al. (2005) that manipulated heterotrophs, only 5 studies manipulated predator diversity (Naeem et al. 1994, Petchy 1999, Wardle et al. 2000, Bradford et al. 2002, Downing and Leibold 2002). Unfortunately, all of these studies were not designed to test the effect of predator diversity on prey consumption, but rather the entire ecosystem consequences of simultaneous changes in diversity at multiple trophic levels. For this reason, there is no way to determine the effect of increasing predator density on prey consumption. Likewise in the Duffy et al. (2005) review a total of 14 studies included three trophic levels, but again three of these were designed to test the entire ecosystem consequences of simultaneous changes in diversity at multiple trophic levels

(Naeem et al. 1994, McGrady-Steed et al. 1997, Downing 2005). Three additional empirical studies in this review were designed to test how the presence or absence of a third trophic level modified a BEF relationship (Mikola and Setälä 1998, Mulder et al. 1999, Wojdak 2005). Interestingly, all three studies found that the mere presence of a third trophic level modified the relationship between increasing diversity and ecosystem function, reinforcing the importance of incorporating predator-prey interactions into empirical BEF studies.

A total of six studies (30%) in Duffy et al. (2005) review specifically manipulated predator diversity to measure resulting prey consumption. The other four review/analysis included at least some experiments in which predator diversity was manipulated, the proportion of predator-prey studies ranged from 10% at most (Cardinale et al. 2006a), to only 0.8 % (Balvanera et al. 2006). Thus, current knowledge of BEF, as it relates to predator diversity and prey consumption, is based on only 12 studies (see Table 1).

All of the above papers concluded that as diversity increases so too did ecosystem function, but results are idiosyncratic when only studies that manipulate diversity of the third trophic level are considered (table 1). Although plants can change their physiology and resource allocation due to competition and chemical interactions, predators and prey can certainly draw from a more complex pallet of behaviors, e.g. they can migrate (and eat). These relatively more complex interactions can give rise to behavior changes of both predators and prey in predator-prey systems (Werner and Peacor 2003). It is clear that more empirical research is needed to determine the relationship between predator diversity and prey consumption. Knowing this relationship is not only important for making management decisions for conservation, but is also necessary to predict when a diversity of predators is needed for biological control of pests (Snyder et al. 2005). Given that the magnitude and direction of the effects of increased predator

diversity on prey consumption appear to be system dependent (Bruno and Cardinale 2008), a fruitful step might be to determine what mechanisms are responsible for the effect of increased predator diversity on prey consumption. A mechanistic understanding of why diversity may or may not matter can help researchers predict when and where conserving diverse or single predators is necessary for pest suppression (Snyder et al. 2005, Ives et al. 2005). We can do this by developing empirical experiments designed to test explicitly for possible mechanisms (e.g. Finke and Snyder 2008). Next I review all empirical predator-prey studies I am aware of that manipulate/observe the effects of increasing predator diversity on prey. I review only those studies that include >2 species of predators in their high diversity treatment. I recognize there are many 2-species predator studies that can give important insight into interactions between multiple species. For example, Losey and Denno (1998) showed how predators can act synergistically to improve pest suppression. Siddon and Witman (2004) highlighted the importance of predator behavior and habitat complexity in mediating multi predator interactions, and Griffen (2006) pointed out the importance of using the appropriate experimental design (for reviews, see Sih 1998, Schmitz 2007). These insights can inform BEF researchers and aid in determining the mechanisms responsible for emergent changes in prey consumption in high diversity treatments.

Effects of increasing predator diversity on prey consumption

For ease of discussion I have summarized all 19 predator-prey diversity studies in Table 2. Considering all empirical studies together, two clear patterns arise. First, a negative effect of increasing predator diversity on prey consumption is relatively rare. Second, increasing the

complexity of a study system to reproduce the complexity typical of real world food webs, (such as: multiple predator densities, including studies with differing numbers of trophic levels, varying diversity of multiple trophic levels) causes idiosyncratic results in the relationship between increased predator diversity and resulting prey consumption.

One study provided clear evidence for decreased prey consumption with increasing diversity (Cardinale et al. 2006b). Another study reported antagonism due to intra guild predation, but because this study included only one predator species in monoculture, a diversity effect is unknown (Finke and Denno 2004). All other studies had positive (5 studies), neutral (4 studies), or a combination of effects depending on multifactor treatments (7 studies). Of the 7 studies that found an effect of diversity depended on an additional variable, only one included a negative relationship (Finke and Denno 2005). Thus a conservative estimate of how often these studies found that greater predator diversity led to decreased prey consumption is 6% of the time and no more than 11%.

Frequently the effect of increased predator diversity on ecosystem function depends on a separately manipulated variable; this was true for 41% (seven studies) of all studies in table 2. the studies summarized in table 2were almost evenly split between positive (29%) and neutral (23%) diversity effects. I will discuss each of the 7 studies in the same order they are found in table 2. A survey of parasitism rates in grasslands found no relationship between increased parasitoid diversity and rates of parasitism, but these rates decreased as food web complexity or herbivore diversity increased (Montoya 2003). When pea aphid host plant diversity was manipulated as well as predator diversity, increased diversity of the predators had a positive effect on prey consumption only when plants were in monoculture. By contrast, there were no effects of increasing predator diversity on pea aphid consumption in plant polyculture (Aquilino

et al. 2005). In another study (Finke and Denno 2005), when strict predators were included in diverse predator treatments, the effect of increasing diversity was additive, whereas, with the inclusion of an intra-guild predator, the diverse predator community consumed fewer prey than expected from additive predator effects. Wilby et al. (2005) only found a positive relationship between increasing predator density on prey consumption when the prey was a holometabolous insect, whereas there was no effect when the insect pest was an hemimetabolous insect (Wilby et al. 2005). A positive effect of increased parasitoid diversity on parasitism was found only for communities of specialist parasitoids, but not for generalist parasitoids (Finke and Snyder 2008). Two papers simultaneously manipulated predator density and diversity and both found that at low predator densities there was no effect of increasing predator diversity on prey consumption, whereas at higher densities both found a positive effect of increasing predator diversity prey on consumption (Griffin et al. 2008, Griffiths et al. 2008). Thus, it is becoming clear that predator/prey identity, habitat structure, predator–prey ratios, food web complexity, and likely many other system-specific attributes modify the relationship between predator diversity and prey consumption. In order to advance BEF studies and predict when diversity matters, we must first incorporate realistic complexity into our studies. We must also determine general mechanisms for the effects of increased diversity on ecosystem function, especially with systems that include predators.

Mechanisms for BEF relationships in predator-prey studies

Though most studies in table 2 suggest possible underlying mechanisms, few have been designed to test such mechanisms. Two studies included (table 2) could not or did not directly compare the

effect of predator diversity for these studies there was no way to determine the effects of increasing predator diversity *per se* on pest suppression, (Finke and Denno 2004, Bruno and O'Connor 2005).

When neutral diversity effects are reported, this is typically interpreted as evidence that the predator species are functionally equivalent (Rodriguez and Hawkins 2000, Sokol-Hessner and Schmitz 2002, Montoya 2003, Byrnes 2006); Straub and Snyder (2006) acknowledge that the short length of their experiment might not have been adequate to detect a diversity effect, even though their study ran longer than any of the above-mentioned studies. It remains possible that neutral effects can arise as artifacts of experimental design such as including predators at one specific density (Griffen 2006, Griffin et al. 2008, Griffiths et al. 2008). In addition, if only prey consumption is measured the actual ecosystem function that matters could be missed altogether. Prey density is often measured as a proxy for ecosystem function with the assumption that fewer herbivores will cause an increase in primary production; this is not always the case. Brynes (2006) showed, in a marine system, that even in the absence of a numerical response in prey density, diverse predator communities elicited a behavioral response in the herbivores which decreased feeding on kelp and caused a trophic cascade (Byrnes 2006).

Five of the studies in Table 2 could only infer general mechanisms for the positive effect of diversity (Cardinale 2003, Aquilino et al. 2005, Wilby et al. 2005, Snyder et al. 2006, Snyder et al. 2008). Aquilino et al. (2005) showed that the positive effect of predator diversity attenuated in plant polycultures, and Snyder et al. (2008) showed that multiple prey species did not modify the positive relationship between increased predator diversity and prey consumption. Cardinale (2003) proposed that the positive effect of predator diversity on the consumption of pea aphid was due to facilitation between two predators, mediated by the presence of a second non-

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manipulated prey species. However this mechanism was never specifically tested (Cardinale et al. 2003). Wilby et al. (2005) hypothesize that prey with differing morphological and behavioral attributes could modify a predator diversity effect. Indeed, a significant positive effect of diversity was found with only one of the prey species, the proposed mechanisms for the positive effect of diversity were partitioning of resources, release from intra specific competition in high diversity treatments, and perhaps facilitation. Thus Wilby et al. (2005) proposed every mechanism that has been theorized to drive positive relationships between increasing diversity and increasing ecosystem function. Five of the studies in table 2 proposed a mechanism in reference to experimental design or follow-up laboratory experiments (Finke and Denno 2005, Cardinale et al. 2006b, Van Son and Thiel 2006, Griffiths et al. 2008, Straub and Snyder 2008). When intra-guild predators were included in diverse communities the relationship of increasing predator diversity was negative for plant hopper suppression, and the magnitude of antagonism increased with increasing diversity of intra-guild predators (Finke and Denno 2005). Cardinale et al. (2006b) found a negative effect of increased lady beetle diversity on pea aphid consumption. In the laboratory, these authors found that two of the three predators used in the field were less effective because they were displaced from the premium feeding sites where prey aggregated, when they foraged with heterospecific predators. But it was not clear if this effect was due to diversity *per se* or increased predator densities in the high diversity treatments because these factors were not isolated in the design. Van Son and Thiel (2006) were able to quantify both where predators fed and prey behavior, in low versus high predator diversity treatments, leading to their conclusion that a positive effect of increased predator diversity on amphipod consumption was due at least in part to predator facilitation due to a change in prey behavior. Griffiths et al. (2008) varied predator density and diversity; this design allowed them to conclude

that at low predator density identity effects of each predator were strong and there was no effect of increasing predator diversity when predator density was low. However, like Wilby et al. (2005) they proposed every possible mechanism to explain the positive relationship of increased predator diversity effects at high predator density (Griffiths et al. 2008). Finally Straub and Snyder (2008) varied plant species and predator diversity, and found a positive effect of diversity on each of two plant species. Subsequent lab experiments revealed that this effect could be due to resource partitioning as predators differed spatially in where they foraged on the plants. In addition, another mechanism they proposed was increased foraging time on the plants in high diversity treatments (Straub and Snyder 2008).

Two studies in Table 2 are unique in providing strong evidence for a general mechanism for positive effects of diversity, and resource partitioning (Finke and Snyder 2008, Griffin et al. 2008). Both studies tested specifically for mechanisms. Finke and Snyder (2008) manipulated diversity of parasitoids, and patterns of resource use within each species via predator host fidelity. This allowed the authors to separate species identity effects from pattern of resource use. What they found was that parasitism increased only when the species richness of parasitoids with individually narrow resource use was increased. In this experiment, a positive effect of diversity was due to resource partitioning only, as the same species richness did not increase resource use when all parasitoid species individually had access to the entire resource space (Finke and Snyder 2008). Griffin et al. (2008) manipulated predator diversity and predator density, but unlike the experimental design employed by Griffiths et al. (2008), the prey base included multiple species and sizes. Thus, the relative consumption of each prey species could be quantified at the end of the experiment. Like Griffiths et al. (2008), Griffin et al (2008) found that at low predator density there was no effect of increasing predator diversity; a positive

relationship between predator diversity and prey consumption was detectable only at high predator densities. Nonetheless, these authors were able to show that predators were likely increasing consumption in high diversity treatments though a partitioning of prey resources. This was evidenced by a difference in prey preference by individual species when they foraged with conspecifics, versus a broadening of numbers of prey species consumed in high diversity treatments. In addition, the multiple predator densities used in this experiment allowed the authors to compare changes in per capita consumption as predator density increased. Per capita consumption decreased with increasing predator density in single species treatments, but not in diverse predator treatments. Coupled with the evidence for prey preference differences between predator species, this is consistent with a partitioning of resources between predator species. This is because in a substitutive experimental design, when each predator species differs in prey preference, as a single species increases density they will deplete the prey items they prefer to feed on at a lower total predator density more rapidly than they will in a diverse predator community. This occurs because the diverse community is made up of fewer conspecifics feeding on the same prey items. Without the evidence of predator feeding preferences this alone would not be clear evidence of resource partitioning, as it could also result from a release of antagonistic intra-specific interactions other than competition for the same prey items (Griffin et al. 2008).

As only two out of 17 studies provide strong evidence for the mechanisms responsible for the effects of increasing predator density on prey consumption, it is clear that there is a large gap in our understanding of why, how and when predator diversity affects ecosystem functioning. Until we understand the mechanisms responsible for the many possible relationships between predator diversity and prey consumption, we will be unable to predict when increased predator

diversity will improve the control of prey. This ability to predict when it is preferable to preserve a diverse predator community or just key predator species to improve pest suppression is imperative for conservation biological control programs.

This dissertation

One approach to finding mechanism(s) responsible for a given effect of predator diversity on prey consumption is to use a system with a known positive/negative/neutral effect of predator diversity on prey consumption, and vary factors to determine how each modifies prey consumption. In our laboratory, we have examined the relationship between diversity among a guild of insect predators, and the strength of resulting suppression of shared aphid prey in a collard (*Brassica oleracea*) system. In all studies conducted in this system, we have found a positive effect of increasing insect predator diversity on prey (aphid) consumption (Snyder et al. 2006). I am seeking a better understanding of the mechanisms contributing to improved herbivore suppression with greater predator biodiversity in this system. In large field cage experiments, I manipulated either the diversity of the prey base or overall predator density. In both cases, these manipulations were crossed with predator diversity to determine if the direction or magnitude of aphid suppression changed. Such a change could provide insight into a general mechanism.

Theory predicts that greater prey diversity will foster the emergence of complementary predator feeding patterns and weaken any negative effects of intraguild predation (van der Heijden 1998, Klironomos 2000, Naeem 2000). Indeed, some empirical studies support the theory that a diverse prey base can be the mechanism for positive diversity effects in high

diversity treatments (Cardinale 2003, Wilby et al. 2005). When a disruptive effect of predator

diversity is found, experimental predator-prey communities often pair a simplified prey base of a

single shared prey species with the inclusion, at high diversity levels, of a strong intraguild

predator that attacks the herbivore's most effective predator (Ives et al. 2005). In contrast, in

studies where multiple prey species are included in experimental arenas, top-down suppression

of herbivore densities generally strengthens with greater predator diversity (Cardinale et al. 2003,

Aquilino et al. 2005, Wilby et al. 2005, Byrnes 2006, Snyder et al. 2006). In this second group of

studies, improved control at higher diversity levels is usually attributed to predator

complementarity, with different predators exhibiting preferences for different prey stages or

species, such that overall prey exploitation is greatest when many enemy species are present

together. Together, these results are consistent with predictions from theory that greater prey

diversity will both foster the emergence of complementary predator feeding patterns and weaken

any negative effects of intraguild predation (Ives et al. 1996, Wilby and Thomas 2002, Briggs

and Borer 2005). Thus, a positive relationship between predator diversity and improved prey

suppression might be most clearly realized when several prey species are present, if a diversified

prey base allows complementarity among predators to be realized. In the study described in

Chapter 2, I used field cages to examine the effects of including multiple prey species on

predator diversity by simultaneously manipulating presence or absence of multiple prey (one or

two species) and predator diversity (monoculture or polyculture) in two experiments. In these

experiments I found that the strength of aphid suppression always increased with greater predator

biodiversity, but this effect was independent of prey species diversity or identity. This suggests

that the benefits of predator diversity for prey suppression were mediated by interactions within

the predator community, such that a diverse resource base was not necessary to yield a positive relationship between predator biodiversity and effective herbivore suppression.

Changes in overall predatory density could interact with the magnitude of a predator diversity effect on prey consumption by a variety of ways. First, the changes in predator density can have non-linear effects on per-capita prey consumption (Osenberg et al. 1997, Cardinale et al. 2006b). Also, an effect of diversity can only be detected empirically when prey are limiting to at least one of the predator species. Because substitutive designs hold overall predator density constant, they are the sensitive to this. In addition to being able to modify the relationship of predator diversity and prey consumption, varying overall predator density can also help to indicate general mechanisms for the positive effect of diversity found in this system.

In typical BEF studies, which use a substitutive design, we cannot determine what process is responsible for an observed pattern as they confound reduction of intraspecific density with increasing interspecific density in high diversity treatments (Connolly 1986,1988 Jolliffe 2000). Likewise when predator-prey BEF studies use an additive design (e.g.Cardinale et al. 2003, Finke and Denno 2004, 2005, Cardinale et al. 2006b) , we cannot distinguish if the effect of diversity is due to non-linear per-capita consumption or non-additive interactions, because predator manipulations are not done at multiple densities (Allison 1999, Cardinale et al. 2006b). Therefore in the research described in Chapter 3, I simultaneously varied predator density and diversity to determine whether predators are able to increase ecosystem function in diverse communities because of a release from intra-specific competition, e.g. niche partitioning or emergent synergistic interactions. This design is unique to predator prey studies. There are only two studies known to this investigator that manipulate predator diversity and density simultaneously and both limited predator density to only two densities (Griffin et al. 2008,

Griffiths et al. 2008). This precludes the other studies from detecting non-linear effects of increasing predator diversity.

Synergism and a release from intra-specific competition are two processes that can lead to increased resource use in diverse communities. Synergism is super-additive and occurs when one species increases the resource use of another species (Connell 1978, Losey and Denno 1998, Sih et al. 1998)). A release from intra-specific competition should be no more than additive and occurs when species use resources differentially so that a greater proportion of a resource base is available for consumption in diverse communities. With complete prey partitioning each predator species attacks a unique subpopulation of prey. For this reason at a relatively low density any single predator species will entirely deplete the prey subject to its attack, whereas relatively high predator densities must be reached before a diverse predator community fully exploits its broader base of vulnerable prey. If resource partitioning is the mechanism responsible for increased prey consumption with increased predator diversity, we would expect that multi-enemy assemblages will continue to extract resources at a density above which predators in monoculture have entirely depleted the prey available to them. We found that aphid suppression always improved with greater predator diversity. However, the magnitude of the difference in suppression between predator monoculture and polyculture treatments grew with increasing predator density. For predator polycultures the strength of aphid suppression roughly quadrupled, but was unchanged for predator monocultures, with a 4-fold increase in total predator density. These results are consistent with resource partitioning among constituent predator species or a release from intraspecific interference, as exploitation of prey by single predator species, but not diverse predator communities, rapidly plateaued with growing predator density.

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Table 1   Summary of predator prey studies included in 5 review/meta-analyses papers

Effect of increasing predator diversity on prey consumption

Review / Meta Analysis	Positive relationship	Neutral relationship	Negative relationship	Relationship depends
(Hooper 2005)	Cannot determine	Cannot determine	Cannot determine	Cannot determine
(Cardinale et al. 2006a)	Total of 3 studies: 1.(Bruno and O'Connor 2005) 2.(Cardinale et al. 2003) 3. (Snyder et al. 2006)	Total of 2 studies: 1.(Byrnes 2006) 2.(Straub and Snyder 2006b)	Total of 1 study: 1.(Cardinale et al. 2006b)	Total of 3 studies: 1.(Aquilino et al. 2005): positive when system was in plant monoculture and neutral in plant poly 2.(Wilby et al. 2005): positive for holometabolist and neutral for a hemi-metabolous insect pests 3.(Finke and Denno 2005): no different than additive w/ strict predator richness and negative with intra guild predation increasing pred richness.
(Balvanera et al. 2006)	0 studies	Total of 1 study: 1.(Rodriguez and Hawkins 2000)	Total of 0 study:	0 studies
(Stachowicz et al. 2007)	Total of 1 study: 1. (Bruno and O'Connor 2005)	Total of 1 study: 1. (Byrnes 2006)	Total of 1 study: 1.(Finke and Denno 2004)	Total of 1 study: 1. (Finke and Denno 2005): (please see above)
(Dufffy et al. 2007)	Total of 3 studies: 1.(Bruno and O'Connor 2005) 2.(Cardinale et al. 2003) 3. (Snyder et al. 2006)	Total of 1 study: 1. (Byrnes 2006)	Total of 1 study: 1.(Cardinale et al. 2006b)	Total of 3 studies: 1. (Wilby et al. 2005): (please see above) 2. (Finke and Denno 2005): (please see above) 3. (Aquilino et al. 2005) (please see above)
Total W/O repeats	3	3	2	3

Table 2. Summary of Biodiversity and Ecosystem Function predator prey studies

Study	System	Type	Organism manipulated	Response measured	# of trophic levels	Diversity effect	Proposed mechanism	Experimental design
Rodriguez & Hawkins 2000	Grassland	Observational	No manipulation	Parasitism rates on herbivorous wasp	3	Neutral	Possibly all species of the parasitoids studied were in one functional group and thus no partitioning of resources could occur	Survey
Sokol-Hessner and Schmitz 2002	Old field	Field cage	Manipulated 3 spider species	Grasshopper density	3	Neutral	Predators substitutable	Substitutive
Cardinale et al. 2003	Agriculture alfalfa	Field cage	3 insect predators: Ladybird beetle, damsel bug, and an aphid parasitoid	Pea aphid density	3	Positive	Facilitation due to presence of second unmanipulated herbivore	Additive
Montoya et al 2003	Grassland	Open field sampling	No manipulation	Parasitism rates on herbivorous wasp	4 to 5	Depends: neutral between parasitoid diversity and parasitism, negative between herbivore diversity/increased food web complexity and parasitism	None	Survey
Finke and Denno 2004	Coastal salt marsh	Field enclosures and greenhouse	3 spider species and 1 mirid bug	Planthopper density	3	Can't tell only one pred in mono	Antagonism due to IGP	Additive
Aquilino et al. 2005	Agriculture: various pea aphid host plants	Lab microcosm	host plant species and natural enemy species 2 lady beetle species and 1 Nabis	Pea aphid density	3	Depends: positive in plant mono-culture neutral in plant poly-culture	In plant mono-cultures facilitative interactions and/or a reduction in intraspecific competition In plant poly cultures more difficult to locate prey	Substitutive both plants and predators
Bruno and O'Connor 2005	Sea	Aquatic outdoor mesocosm	Predators crab, shrimp, bennies, killifish and pinfish	Herbivores isopod and amphipod densities	3	Can't tell only report presence versus absence of predator not single vers multiple predators on herbivore #	NA	Substitutive

Study	System	Type	Organism manipulated	Response measured	# of trophic levels	Diversity effect	Proposed mechanism	Experimental design
Finke and Denno 2005	Coastal salt marsh	Greenhouse meso cosms	4 spiders and a lady beetle	Planthopper density	3	Depends: no different than additive w/ strict predator richness and negative with IGP increasing pred richness.	Intraguild predation	Additive
Wilby et al. 2005	Agriculture: rice fields	Greenhouse microcosms	Wolf spider, ladybeetle, cricket, and a mirid plant bug	Planthopper and moth density	3	Depends: Positive for moth neutral for planthopper	Functional complementarity	Substitutive
Byrnes et al 2006	Kelp forests	Outdoor mesocosms	2 species of crabs, and 1 sun star	Herbivores density 2 species of snails, 2 species of sea urchin, and a kelp crab	3	Neutral	No density effect on herbivore but there was a positive trophic cascade due to herbivore prey modified behavior	Substitutive
Cardinale et al. 2006 b	Agriculture: alfalfa	Field cages	3 lady beetle species	Pea aphid density	3	Negative	Lab experiment showed interference competition	Additive
Snyder et al. 2006	Agriculture: collards	Field cages	2 predatory bug species, 2 lady beetle species, and a parasitoid wasp	Green Peach, and cabbage aphid densities	3	Positive	Insurance effect overyeilding only occurred in mixtures with H. convergance or D. rapae.	Substitutive
Straub and Snyder 2006	Agriculture: potato	Field cages	Experiment 1: 2 predatory bugs, lady beetle, spider. and ground beetle experiment 1: 2 predatory bugs, lady beetle, and a parasitoid wasp	Green peach aphid density	3	Neutral for both experiments	Possibly experiments too short to see diversity effects Coccinellid had strong effects	Substitutive
Van Son And Thiel 2006	Intertidal boulder	Marine aquatic microcosms	Manilpulated predators: nemertean shrimp, and juvenile fish	Amphipod density	3	Positive	Predator facilitation	Substitutive

Study	System	Type	Organism manipulated	Response measured	# of trophic levels	Diversity effect	Proposed mechanism	Experimental design
Finke and Snyder 2008	Agriculture: radish	Field cages	3 parasitoids species but also generalists versus specialists within each species via predator host fidelity	Green peach, cabbage and turnip aphid densities	3	Depends: positive with specialist and neutral with generalists	Unambiguous evidence for resource partitioning	Substitutive
Griffin et al. 2008	Intertidal food web	Sea water outdoor mesocosms	Diversity and density of predatory crabs	Barnacle, mussels, periwinkles, topshells, and limpets (two size classes [small and large] were used for every prey species except barnacles	3	Depends: positive only at high predator density	Indirect evidence for niche partitioning (because couldn't measure species specific resource use in poly)	Substitutive
Griffiths et al.2008	Agriculture: wheat	Lab mesocosm	Diversity and density of: lady beetle, rove beetle, predators bug, and lace wing	Rose-grain aphid density	3	Depends: positive at higher densities	Strong species identity effects effects especially at low diversity but at higher diversity caused by several non-exclusive mechanisms: relaxation of intra-specific interfere	Response surface
Snyder et al. 2008	Agriculture: collards	Field cages	Predatory bug, 2 lady beetle species, and a parasitoid wasp also manipulated prey diversity green peach, and cabbage aphid	Green Peach, and cabbage aphid densities	3	Positive	Predator diversity effects not influenced by prey diversity, concluded possible niche partitioning but independent of prey species id	Substitutive
Straub and Snyder 2008	Agriculture: potato and collards	Field cages greenhouse for mechanism	Predatory bug, 2 lady beetle species ,and a parasitoid wasp also manipulated host plant diversity potato and collards in	Green peach aphid density	3	Positive on both plants	Green house experiment showed a difference in spatial foraging of predators and predators spent more time foraging on plants in high diversity treatments	Substitutive

CHAPTER TWO

Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities

Gretchen B. Snyder, Deborah L. Finke, and William E. Snyder

Department of Entomology, Washington State University, Pullman WA 99164 USA

Corresponding Author:
Gretchen B. Snyder
Department of Entomology
Washington State University
Pullman, WA 99164-6382
Phone: 509-335-3724
Fax: 509-335-1009
gbsnyder@wsu.edu

Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities

Abstract

By

Gretchen Beth Snyder

Washington State University

A positive relationship between predator biodiversity and improved pest suppression might be most clearly realized when several prey species are present. In two field experiments we manipulated diversity both within a guild of predatory insects (one versus four predator species) and within the guild of phloem feeding prey (one versus two aphid species present). The strength of aphid suppression always increased with greater predator biodiversity, but this effect was independent of prey species diversity or identity, and no niche differentiation for aphid species was apparent among the predator species. This suggests that either niche partitioning among predators occurred but was not based on prey species identity or that the benefits of predator diversity for biological control were mediated by interactions within the predator community, such that a diverse resource base was not necessary to yield a positive relationship between predator biodiversity and effective herbivore suppression.

Introduction

Agroecologists have long proposed that the lack of biodiversity typical of agricultural

monocultures encourages the dramatic pest outbreaks so common in these systems (Pimentel,

1961). With movement towards organic agriculture and related approaches under the larger

heading of sustainable agriculture, biodiversity among both herbivores and predators generally

increases (Bengtsson et al., 2005; Hole et al., 2005). Similarly, arthropod biodiversity often

grows when crop monocultures are replaced by polycultures (Andow, 1991), and when

landscapes encompass a variety of habitats rather than being dominated by large cropping fields

(Tscharntke et al., 2005). Greater biodiversity seems to correlate with a reduced frequency of

pest outbreaks (e.g., Letourneau and Goldstein, 2001), but the mechanism underlying these

results is not always clear. A pressing challenge for agroecologists is to identify aspects of

biodiversity that are beneficial for agriculture, and that might be enhanced as part of

conservation biological control or other pest management schemes (Altieri, 1991).

However, it is unclear whether greater natural enemy diversity is always desirable. Indeed,

in some predator-prey communities where intraguild predation is common, herbivore

suppression weakens, rather than strengthens, when more predator species are present

(Rosenheim et al. 1993, Snyder and Ives 2001, Snyder and Wise 2001, Finke and Denno 2004,

Bruno and O'Connor 2005, Finke and Denno 2005). When a disruptive effect of predator

diversity has been reported, the experimental predator-prey communities often pair a single

shared prey species with a diverse predator guild that includes a strong intraguild predator that

attacks the herbivore's most effective predator (Ives et al. 2005). In contrast, in studies where

multiple prey species are included in experimental arenas, top-down suppression of herbivore densities generally strengthens with greater predator diversity (Cardinale et al. 2003, Aquilino et al. 2005, Wilby et al. 2005, Byrnes 2006, Snyder et al. 2006). In this second group of studies improved control at higher diversity levels is usually attributed to predator complementarity, with different predators exhibiting preferences for different prey stages or species, such that overall prey exploitation is greatest when many enemy species are present together. Together, these results are consistent with predictions from theory that greater prey diversity will both foster the emergence of complementary predator feeding patterns and weaken any negative effects of intraguild predation (Ives et al. 1996, Wilby and Thomas 2002, Briggs and Borer 2005). However, predator diversity studies in biological control systems have manipulated predator species richness only, and not prey diversity, such that reciprocal effects of predator and prey diversity on herbivore suppression have not been examined explicitly.

We have been examining the relationship between diversity among a guild of arthropod predators and the strength of resulting suppression of shared aphid prey. In one set of experiments where a single herbivore species, the green peach aphid [*Myzus persicae* (Sulzer)], was the only prey species present, and potato (*Solanum tuberosum* L.) was the host plant, the strength of aphid suppression was unaffected by predator species richness (Straub and Snyder 2006b). In contrast, in a second series of experiments where two prey species, again the green peach aphid but also the cabbage aphid [*Brevicoryne brassicae* (L.)], were always included together and collards (*Brassica oleracea* L.) was the host plant, aphid suppression was invariably more effective when multiple predator species were present (Snyder et al. 2006). One obvious difference between these two studies that might underlie the different predator diversity-herbivore suppression relationships was the differing number of prey species included; one aphid

species on potato (green peach aphid) versus two aphid species on collards (green peach aphid and cabbage aphid). Theory predicts that, if predators differ in their effectiveness at capturing different prey species, a diverse prey community will increase the importance of a diverse predator community for effective biological control (Wilby and Thomas, 2002; Ives et al., 2005). This is because only a diverse predator community will include the most effective predators of all prey species. We predicted that the positive effect of increasing predator diversity on prey consumption in our collard system might depend on the inclusion of multiple prey species.

Of course, there were many differences other than prey diversity among our earlier series of experiments in potatoes and collards, including different host plants, time of year the experiments were conducted, etc., limiting what can be gleaned from comparisons between the two to ascertain the effect of prey diversity. Here we report the results of two field experiments in which we manipulated simultaneously, on a single host plant species, diversity of both predators and their shared aphid prey. Our goal was to test the hypothesis that greater predator diversity would strengthen overall aphid suppression in the presence of two aphid species, but not a single aphid species.

Materials and Methods

Natural History

Two common aphid species, green peach and cabbage aphids, attack the plant *Brassica oleracea* (cabbage and its relatives) throughout much of the world. The green peach aphid lacks any obvious physical or behavioral defense, and generally is randomly dispersed on the undersides of lower plant leaves (Snyder et al. 2006). In contrast, the cabbage aphid aggregates and covers

itself with a waxy secretion as a physical defense, and occurs primarily on the growth tips and upper leaves (Snyder et al. 2006). These differences could lead to differing susceptibility of the two aphid species to predator species that vary in hunting location or ability to circumvent a particular defense. Thus, a diverse predator community, including species with diverse hunting styles, might enhance herbivore suppression when the two aphid species co-occur. Within the growing season both aphids reproduce parthenogenetically and rapidly, with populations increasing 10-fold in as little as 10 days at our field site in eastern Washington, USA (Snyder et al. 2006). Locally, the aphids are attacked by a diverse community of predators, dominated numerically by several true predators including the bug *Nabis* spp. and the coccinellid beetles *Coccinella septempunctata* L. and *Hippodamia convergens* Guérin-Méneville, and also a parasitoid wasp, *Diaeretiella rapae* (McIntosh) (Snyder et al. 2006). These natural enemies span a range of hunting styles, including a sit-and-wait predator (*Nabis*), active searchers (the coccinellids), and an endoparasitoid (*Diaeretiella*). This diversity of foraging strategies might lead to predators differing in their ability to capture particular aphid species, such that any benefits of predator diversity for biological control would be heightened when a multi-species prey community was present.

Field Experiments

Our two field experiments differed only in the prey species in prey mono-culture treatments, but otherwise shared a common design. In both, we conducted fully-factorial manipulations of both prey diversity (one versus two aphid species) and predator diversity (one versus four predator species). Both experiments were conducted at the Washington State University Research Station in Othello, WA. Our experimental units were 2 x 2 x 2 m cages covered with fine mesh

screening. Aphids and parasitoids used in our experiments were collected from colonies maintained in the field, while the predators were hand or D-vac collected from neighboring agricultural fields. Details of cage construction and insect handling were identical to those provided in Snyder et al. (2006).

Eight 21-d-old collard plants were transplanted into cages on 3 August 2005 for Experiment 1, and on 17 August 2006 for Experiment 2. Ideally, within both experiments our aphid manipulation would have included two low prey diversity sub-treatments, consisting of each aphid species in monoculture, along with a polyculture treatment with the two aphids species together. Because of limitations in labor, space and materials, we used the green peach aphid as the sole prey species in our prey Monoculture treatment in Experiment 1, and the cabbage aphid as the sole prey species in Monoculture in Experiment 2; each experiment included an aphid Polyculture treatment with both aphid species present together. Two d after plants were transplanted they were infested with wingless aphids by releasing 20 aphids onto each plant. Aphids were manipulated within a substitutive design, such that cages received either 160 aphids of the same species in prey Monoculture, or 80 aphids of each of the two species in prey Polyculture. After allowing 48 h for aphids to become established, aphids were counted for the first time (this count immediately preceded predator release, described below, and constituted day 0 of the experiment), and then again on days 11, 19 and 28. Aphids were counted on 4 randomly selected plants per cage for samples on days 0 and 11, and on 2 randomly selected plants per cage on days 19 and 28, such that sampling intensity decreased as aphid densities increased through time (Snyder et al. 2006). We carefully hand-searched all leaves of each plant selected for aphid sampling, and recorded all aphids present.

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In both experiments a Low predator diversity treatment consisted of 6 replicates of each of the four predator species in monoculture (total $N = 24$), while a High predator diversity treatment consisted of 12 replicates where all 4 predator taxa were present together. The experiments also included 8 No-Predator controls where predators were not released. Within our fully-crossed design, half of the replicates of each predator treatment were established in cages housing the aphid Monoculture treatment, and the other half in cages containing the aphid Polyculture treatment. We again utilized a substitutive design for predator manipulations such that all cages received 48 predator individuals, with Low predator diversity cages receiving 48 individuals of the same species and High predator diversity cages receiving 12 of each of the 4 predator species. This density of 6 predators per plant is somewhat below typical total predator densities, and within the range of single-species densities, for each of the predator taxa we examined in local agricultural fields not treated with broad-spectrum insecticides (Snyder et al. 2006). Our experimental design paired constant predator densities across diversity treatments with the appearance of all species at both high and low diversity levels. These design features eliminate confounding "sampling effects" (Huston,1997), wherein particularly efficient consumers are relatively more abundant in high diversity treatments, by insuring that predators occur at the same relative abundance in both low and high diversity treatments (Straub and Snyder, 2006b).

All predators were released into cages as adults because it is the winged adults that typically first colonize agricultural fields (Wissinger 1997). The 28-day experimental period was sufficient to allow slightly less than 2 complete generations (adult to adult) of the parasitoid, and parasitoid mummies were counted concurrent with each aphid survey. Development (adult-adult) of true predators (i.e. those other than the parasitoid) can be completed in ca. 1 month under conditions

typical of our site (Snyder et al. 2006), so that our experimental period encompassed less than one complete generation for true predators. True predators reproduced within our experimental cages, but the immature predators did not molt to adults. The presence of immature true predators increased the likelihood of the occurrence of intraguild predation, and thus enhanced the potential for negative effects of greater predator diversity on pest suppression. True predators (adults and immatures) were counted at the end of the experiment, immediately following the final aphid count on day 28. True predators were collected from all cages by hand-searching all plants in each cage for 15 min/cage, and then again 2 more times after plants were harvested (see below). Hand searching at this intensity effectively recovers most predators (Snyder et al. 2006).

At the final aphid count, collard plants were harvested. Collards were harvested by cutting the base of the main stem flush with the soil surface. Plants were returned to the laboratory, dried in a drying oven at 65° C for 7 d, and then weighed.

Analyses

Aphid population suppression was analyzed using repeated measures MANOVA with a factorial cross of prey (Monoculture versus Polyculture) and predator (Low versus High) diversity. We examined whether predators suppressed aphid populations by comparing total aphid densities (green peach aphids or cabbage aphids only in Monoculture prey treatments; the sum of both green peach and cabbage aphids in Polyculture prey treatments) in cages containing predators (pooled Low + High predator diversity treatments) to those in the No Predator controls; we examined whether the strength of aphid suppression varied with greater predator diversity by comparing total aphid densities in Low vs. High predator diversity treatments. Total aphid densities before predator release were included as a covariate in these analyses. We compared

impacts of different predator taxa on aphids when the predators were in monoculture, final per-capita recovery of predators and parasitoids (number of individuals collected at the last sample / number added initially), and final plant biomass using 2-way ANOVA. Disproportionate predation of one aphid species over the other by different predators would provide evidence of differential resource use. To look for differences among predator species in their impacts on the two aphid species, we calculated the proportion of green peach aphids eaten minus the proportion of cabbage aphids eaten, with proportion eaten for each aphid species calculated as: (mean density of that aphid species in predator-free controls - number of aphids of that species surviving in that cage) / mean density of that aphid species in predator-free controls. With this index a positive value indicated that green peach aphids were attacked at a greater rate than would be expected by their relative abundance.

Results

Because the two experiments differed only in the prey species in monoculture (green peach aphid in Experiment 1, versus cabbage aphid in Experiment 2), and otherwise shared the same design, we present results by response variable for easy comparison between the two studies.

Aphids

Treatment x time interaction terms were never statistically significant and are not discussed here; complete results of the repeated measures analyses are presented in Tables 1-4, and complete time series data for total aphid densities (a single aphid species in prey Monoculture treatments or the sum of both aphid species in prey Polyculture treatments) are presented in Fig. 1.

In both experiments, total aphid densities were significantly lower in the presence of predators, compared to the No Predator controls (Tables 1 and 2, Fig. 2a-b). However, the ability of predators to suppress aphids was not affected by aphid species diversity ($P \geq 0.65$ for aphid

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diversity main and interactive effects in both experiments; Tables 1 and 2, Fig. 2a-b).

Furthermore, in both experiments total aphid densities were significantly lower in the presence of a diverse predator assemblage, compared to predators monocultures (Tables 3 and 4, Fig. 2a-b). In neither experiment, however, did our manipulation of prey species diversity impact the stronger suppression of aphids in diverse than in single-species predator communities ($P > 0.10$ for all aphid diversity main and interactive effects in both experiments; Tables 3 and 4, Fig. 2a-b).

Predators

In Experiment 1, the predator taxa differed significantly in aphid suppression exerted ($F_{3,16} = 6.85$, $P = 0.004$; Fig. 3a), a result driven by stronger aphid suppression by *Coccinella* than by the other predators ($P \leq 0.01$ for all comparisons between *Coccinella* and other taxa, ANOVA followed by Tukey's HSD test; all other comparisons among taxa were $P > 0.95$; Fig. 3a). However, for all predator taxa, the magnitude of aphid control exerted was similar regardless of whether one or two aphid species were present (aphid diversity x predator species interaction: $F_{3,16} = 0.86$, $P = 0.48$). For Experiment 2, predator species did not differ in the magnitude of aphid reduction ($F_{3,16} = 0.762$, $P = 0.53$; Fig. 3b), and aphid suppression was again unaffected by prey treatment (aphid diversity main effect: $F_{1,16} = 0.22$, $P = 0.64$; interaction between predator species identity and aphid diversity: $F_{3,16} = 1.76$, $P = 0.17$; Fig. 3b). The general trend was for predators to feed more heavily on green peach than on cabbage aphid relative to the abundances of these species (Fig. 3c-d), but predator species did not differ significantly among one another in their aphid species preferences in either experiment ($F_{3,8} = 2.57$, $P = 0.13$ and $F_{3,8} = 0.86$, $P = 0.50$ for Experiments 1 and 2, respectively).

At the end of the experiment predator diversity remained significantly higher in High than Low predator diversity treatments in both Experiment 1 (mean species richness = 0.96 $\pm$ 0.04 and 3.50 $\pm$ 0.15 for Low and High, respectively; $F_{1,32}$ = 640.17, $P < 0.001$) and Experiment 2 (mean species richness = 1.00 $\pm$ 0.00 and 3.58 $\pm$ 0.15 for Low and High, respectively; $F_{1,32}$ = 602.98, $P < 0.001$). In Experiment 1, final densities of parasitoid pupae were marginally lower in High than Low predator diversity treatments ($F_{1,14}$ = 4.08, $P = 0.063$; Fig. 2c), but parasitoid densities were unaffected by predator diversity treatment in Experiment 2 ($F_{1,14}$ = 0.02, $P = 0.89$; Fig. 2d). In both experiments parasitoid densities were not significantly affected by either aphid diversity main ($F_{1,14}$ =0.40, $P = 0.54$ and $F_{1,14}$ = 0.50, $P = 0.49$ for Experiments 1 and 2, respectively; Fig. 2c-d) or interactive ($F_{1,14}$ = 1.97, $P = 0.18$ and $F_{1,14}$ = 0.15, $P = 0.71$ for Experiments 1 and 2, respectively; Fig. 2c-d) effects. Although a trend toward higher per capita recovery of true predators in the High predator diversity treatments was observed in both experiments (Fig. 2e-f), predator densities were significantly greater in High than Low only in Experiment 2 ($F_{1,26}$ = 7.28, $P = 0.012$). For true predators, final recovery was not significantly impacted by aphid diversity main or interactive effects in either Experiment 1 ($F_{1,26}$ = 1.18, $P = 0.29$ and $F_{1,26}$ = 0.39, $P = 0.54$ for aphid diversity and aphid x predator diversity effects, respectively; Fig. 2e) or Experiment 2 ($F_{1,26}$ = 0.08, $P = 0.78$ and $F_{1,26}$ = 1.91, $P = 0.18$ for aphid diversity and aphid x predator diversity effects, respectively; Fig. 2f).

Plants

In both experiments, final plant biomass was significantly higher in treatments including predators than in No Predator controls, but plant biomass did not differ between High and Low predator diversity treatments (Tables 5 and 6, Fig. 2g-h). In neither experiment did aphid diversity main or interactive effects impact plant productivity (Tables 5 and 6).

Discussion

We found that total aphid suppression strengthened significantly when predator communities included multiple predator species compared to the average across predator species in monoculture (Fig 2a-b), and this effect was independent of prey diversity. Our experimental design included all predator species, and maintained constant relative abundances of the different species, in both low and high diversity treatments. With these design features no single, particularly effective predator species can disproportionately influence the response of a predator polyculture (Straub and Snyder, 2006b). This is because each species was at one quarter the abundance when in polyculture such that, in the absence of a change in mean per-capita predation rate when mixed with other species, the null prediction is a simple averaging of predation across monocultures of the constituent species (Straub and Snyder, 2006 a,b). A separate issue is whether any single predator species could achieve control equal to that observed by the diverse predator polyculture. For example, in our first experiment *C. septempunctata* in monoculture suppressed aphids to a density similar that the predator polycultures. When such occurs, conservation of the single most effective species could improve biological control as effectively as conserving the entire predator assemblage (Straub and Snyder, 2006a). However, whereas *Coccinella* provided strong suppression in one experiment, diverse predator communities exerted strong control in both experiments, suggesting that predator biodiversity may provide "insurance" (*sensu* Yachi and Loreau [1999]) for effective aphid control.

Consistent with the greater resource exploitation exerted by diverse than monospecific predator communities, we recovered more true predators from predator polycultures than

monocultures, significantly so in the second experiment (Fig 2e-f). Densities of the parasitoid *D. rapae* tended to be lower in predator polycultures than in D. rapae monoculture in the first experiment (Fig. 2c), but were unaffected by predator diversity treatment in the second (Fig. 2d). Thus, predators were no more likely to be negatively than positively affected by inclusion within diverse predator communities. Final plant biomass was significantly greater in treatments including predators compared to predator-free controls, but the greater aphid suppression exerted by diverse than monospecific predator assemblages did not produce a detectable trophic cascade (Fig. 2g-h). While predator diversity clearly impacted the strength of aphid suppression, and sometimes predator performance, these effects appeared to be independent of aphid species identity. Main and interactive effects of our aphid manipulations never significantly altered the strength of aphid suppression, natural enemy survivorship, or the cascading effect of predators on plants (Fig. 2). In summary, while greater predator diversity consistently enhanced herbivore exploitation, these emergent top-down effects of predator diversity were unaffected by any bottom-up effects of prey diversity.

In earlier work we found that greater predator diversity dramatically strengthened aphid suppression on collards housing both green peach and cabbage aphids (Snyder et al. 2006), but did not alter the strength of aphid suppression on potatoes housing the green peach aphid as the sole herbivore species present (Straub and Snyder 2006b). This led us to the hypothesis that it was the relatively diverse, multi-species prey base on collards that heightened the importance of predator complementarity, and thus predator diversity, for effective herbivore suppression (e.g. (Wilby and Thomas 2002, Ives et al. 2005, Wilby et al. 2005). Several lines of evidence suggest that our aphid community manipulations did not influence predator complementarity. Neither the degree of aphid suppression by predators in monoculture, nor predator performance, was

impacted significantly by the availability of one versus two aphid species as potential prey (Fig. 2c-f; Fig 3a-b). Also, when arenas included both aphid species, there was a consistent trend for predators to disproportionately attack green peach aphid. The predators never differed significantly from one another in their tendency to attack one aphid species over the other (Fig. 3c-d). Thus, from the predators' standpoint the two aphid species were equally acceptable as prey – entirely consistent with our inability to find an effect of prey diversity on the relationship between predator diversity and prey suppression. However, power was limited in these comparisons, as each unique predator species x aphid diversity combination was replicated but three times per experiment. It remains possible that a larger-scale experiment would reveal more subtle differences in how individual predator species respond to green peach versus cabbage aphids, as suggested by the trends observed.

Also unresolved is why predator biodiversity plays such different roles in the collards versus potato systems. One possibility is that plant species characteristics, such as differences in plant architecture or chemistry, are mediating the importance of predator biodiversity for effective herbivore suppression. It is well known that plant traits can alter the strength of interactions among resident arthropods (Aquilino et al. 2005, Finke and Denno 2005).

Our experiments were ended when plants were ready for harvest, and thus encompassed an agronomically relevant time scale for this annual-cropping system. However, there were suggestions in the data that experiments run over a longer time period may have revealed impacts of prey species identity and diversity. In the first experiment, reduced survivorship of the parasitoid *D. rapae* within diverse predator communities appeared to be driven primarily by poor parasitoid survivorship when the green peach aphid was the sole prey species (Fig. 2c). Negative impacts of predators on parasitoids that are relatively weak in the short-term can nonetheless

eventually lead to dramatic disruption of herbivore suppression (Borer et al. 2003, Snyder and Ives 2003). Similarly, there was some suggestion in the data, most distinctly in Experiment 2, that aphid impacts on plants were greater with two aphid species present (Fig. 2g-h). If aphid polycultures indeed are more taxing to plants, over longer time scales this could intensify cascading predator effects (Briggs and Borer 2005).

If consumer biodiversity effects are driven by complementarity in exploitation of different resources, then we expect consumer biodiversity effects to be stronger with growing resource diversity (Tiunov and Scheu 2005). This is because a larger number of resource categories create a richer niche space, allowing more distinct niche differentiation along the greater number of resource axes (Hutchinson 1957, Vandermeer 1972). Take for example a case where two herbivores differ in where they reside on plants or in their antipredator defenses (as do the two aphids in our collard system). If different predators differ in where they forage on plants, or in their ability to overcome a defense unique to a particular prey species, then only a diverse predator community will include species very effective at attacking each herbivore species. For this reason, herbivore suppression will be most clearly improved with greater predator diversity when several, different prey species are present together (Wilby and Thomas 2002, Ives et al. 2005, Wilby et al. 2005). However, only a few previous studies have manipulated both resource and consumer diversity simultaneously to explicitly test these ideas, none in predator-prey systems, and those studies reached widely varying conclusions. In our system, we found that consistently stronger aphid suppression with greater predator diversity was largely uninfluenced by prey species identity or diversity. Perhaps, in our predator-prey system any complementarity among predator species due to different hunting styles or patterns of diel activity, for example, simply was insensitive to prey species identity. A second possibility is that intraguild interactions

among predators are driving improved aphid exploitation. If intraspecific predator interference is a stronger force than are negative interactions among different predator species then we would expect, within our substitutive design, overall predator interference to be lowest in our predator polyculture treatments (Aquilino et al. 2005). Though more work is needed to understand why diversity effects at different trophic levels are sometimes reciprocal, sometimes unidirectional, and sometimes weak or non-existent, this study shows that for biological control conserving a diverse predator community improves aphid suppression in the presence of both single and multiple prey species.

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Table 1. For Experiment 1, repeated measures comparison of No Predator control versus pooled (Low + High predator diversity), crossed with Low versus High prey diversity.

Statistic	Predator contrast	Aphid diversity	Predator x aphid	t= 0 aphid density	Model term Time	Time x Pred.	Time x prey	Time x pred. x prey	Time x initial aphid
$F_{1,39}$	17.05	0.087	0.047	4.26					
P	< 0.001	0.77	0.83	0.046					
Wilks' λ					0.81	0.96	0.97	0.98	0.90
$F_{2,38}$					4.52	0.71	0.48	0.35	2.15
P					0.017	0.50	0.62	0.71	0.13

Table 2. For Experiment 2, repeated measures comparison of No Predator control versus pooled (Low + High predator diversity), crossed with Low versus High prey diversity.

Statistic	Predator contrast	Aphid diversity	Predator x aphid	t= 0 aphid density	Time	Time x Pred.	Time x prey	Time x pred. x prey	Time x initial aphid
$F_{1,39}$	33.70	0.005	0.21	6.67					
P	< 0.001	0.94	0.65	0.014					
Wilks' λ					0.94	0.97	0.97	0.96	0.99
$F_{2,38}$					1.20	0.67	0.59	0.86	0.23
P					0.31	0.52	0.56	0.43	0.79

Table 3. For Experiment 1, repeated measures comparison of Low versus High predator diversity, crossed with Low versus High prey diversity.

Statistic	Predator contrast	Aphid diversity	Predator x aphid	t= 0 aphid density	Time	Time x Pred.	Time x prey	Time x pred. x prey	Time x initial aphid
$F_{1,31}$	10.95	0.001	1.68	1.75					
P	0.002	0.98	0.20	0.20					
Wilks' λ					0.72	0.84	0.91	1.0	0.78
$F_{2,30}$					5.94	2.91	1.41	0.014	4.15
P					0.007	0.07	0.26	0.99	0.026

Table 4. For Experiment 2, repeated measures comparison of Low versus High predator diversity, crossed with Low versus High prey diversity.

Statistic	Predator contrast	Aphid diversity	Predator x aphid	t= 0 aphid density	Time	Time x Pred.	Time x prey	Time x pred. x prey	Time x initial aphid
					Model term				
$F_{1,31}$	15.40	1.57	2.70	12.33					
P	< 0.001	0.22	0.11	0.001					
Wilks' λ					0.89	1.00	0.82	0.94	1.00
$F_{2,30}$					1.81	0.039	3.19	1.02	0.061
P					0.18	0.96	0.055	0.37	0.94

Table 5. For Experiment 1, analyses of final plant dry weight.

		Model term		
Predator Contrast	Statistic	Predator effect	Aphid diversity	Predator x aphid
No Predator vs. pooled (Low + High predator diversity)	$F_{1,40}$	4.70	0.78	0.01
	P	0.036	0.38	0.92
Low versus High predator diversity	$F_{1,32}$	0.80	1.05	0.14
	P	0.38	0.31	0.71

Table 6. For Experiment 2, analyses of final plant dry weight.

| Predator Contrast	Statistic	Model term		
		Predator effect	Aphid diversity	Predator x aphid
No Predator vs. pooled (Low + High predator diversity)	$F_{1,40}$	6.50	0.008	0.41
	P	0.015	0.93	0.52
Low versus High predator diversity	$F_{1,32}$	0.72	0.77	0.25
	P	0.40	0.39	0.62

Fig. 1 Total aphid densities in (A) Experiment 1, where green peach aphid occurred in all cages, and (B) Experiment 2, where cabbage aphids occurred in all cages. Data are means $\pm$ 1. s.e.
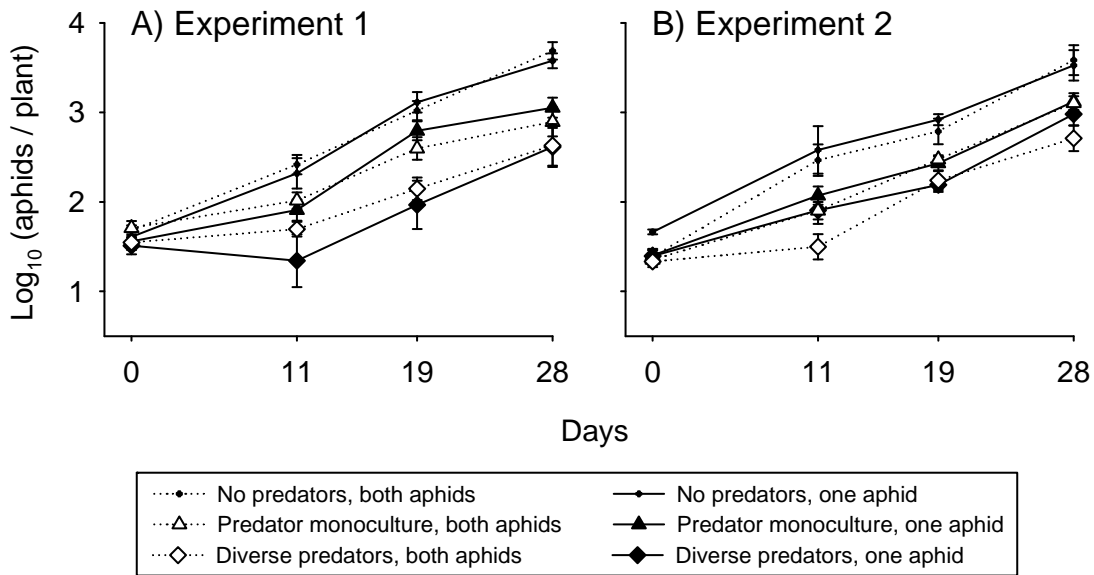
Fig. 2 Mean total aphid density in Experiments 1 (a) and 2 (b), final parasitoid density as a function of initial parasitoid density in Experiments 1 (c) and 2 (d), per capita recovery of true predators at the termination of Experiments 1 (e) and 2 (f), and final plant dry biomass in Experiments 1 (g) and 2 (h). Prey diversity treatments on the x-axis: green peach aphid present in monoculture (GPA), cabbage aphid present in monoculture (CA), and aphid polycultures including both aphid species (Both). Error bars represent means $\pm$ 1 s.e.
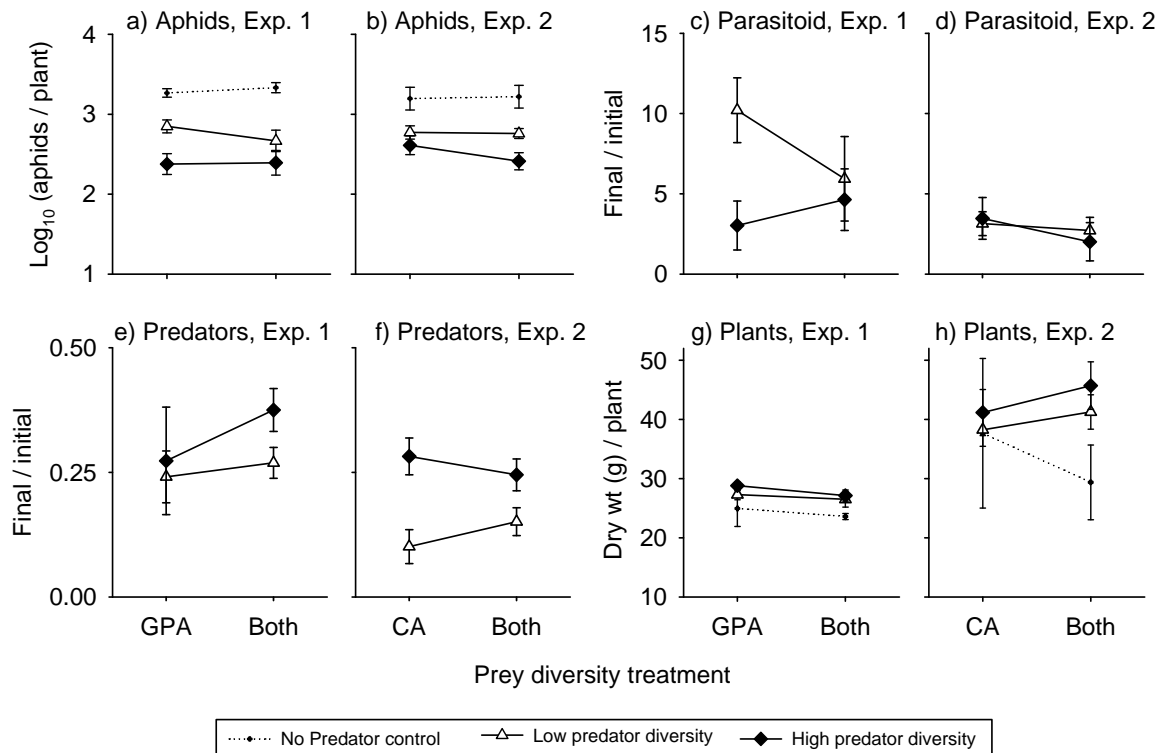
Fig. 3 For each predator species in monoculture, mean total aphid densities for (a) Experiment 1 and (b) Experiment 2, and the proportion of green peach aphids (GPA) consumed minus the proportion of cabbage aphids (CA) consumed for (c) Experiment 1 and (d) Experiment 2. Predator monoculture treatments: *C. septempunctata* (c); *D. rapae* (d); *H. convergens* (h); and *Nabis* spp. (N). Data are the mean aphid densities across the three post-predator-release samples, $\pm$ 1 s.e.
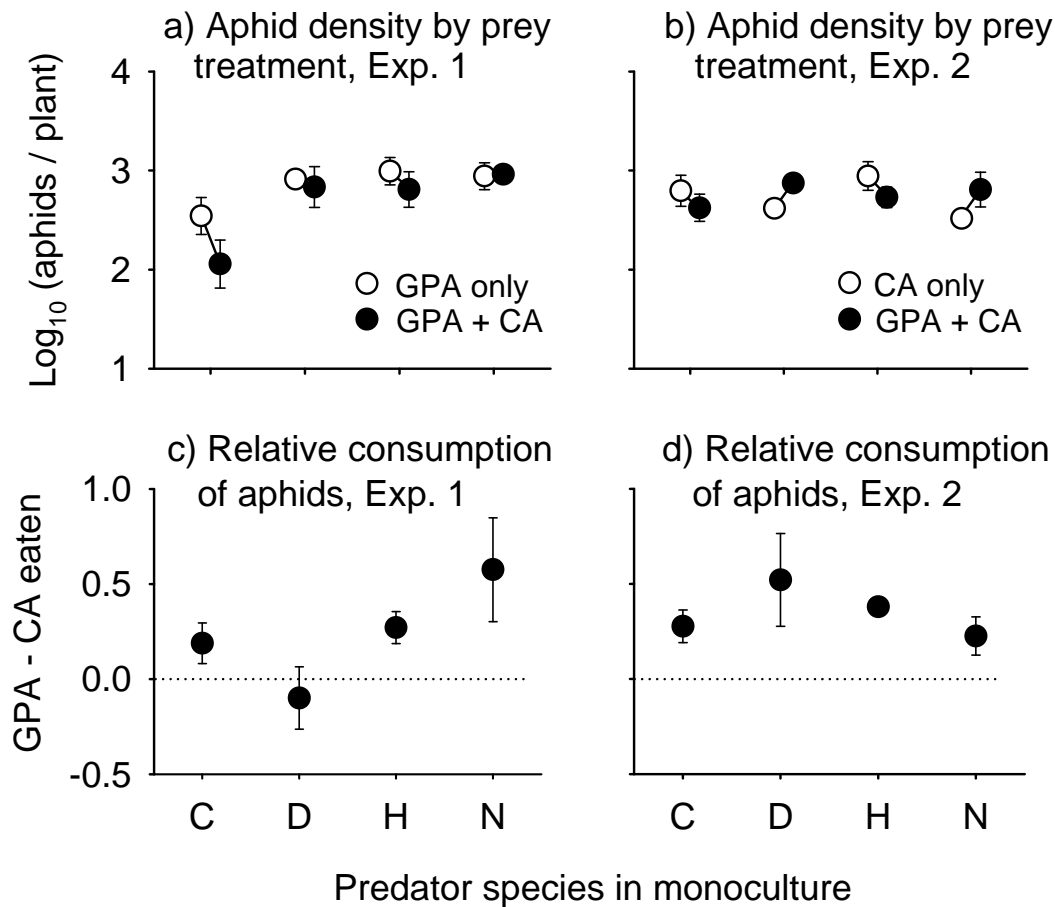
CHAPTER THREE

Release from intra-specific competition drives positive effect of increased predator diversity on prey consumption

Gretchen B Snyder[*] and William E Snyder

Washington State University

WSU Entomology, FSHN, Room 358E, Pullman WA 99164-6382,

 E-mail: gbsnyder@wsu.edu, Telephone: 509-335-8385

Release from intra-specific competition drives positive effect of increased predator diversity on prey consumption

Abstract

By

Gretchen Beth Snyder

Washington State University

Complementarity among consumers is often implicated when resource exploitation increases with greater consumer biodiversity. However, this mechanism has generally proven difficult to demonstrate convincingly. In the field, we simultaneously manipulated diversity and density among a community of aphid predators within a response-surface design to measure resulting effects on aphid densities. Predators in diverse predator communities exerted the strongest aphid suppression, and only among polycultures did aphid suppression continue to strengthen across all predator density levels, consistent with what would be expected if predators were able to partition resources between species or were released from intra-specific competition. In addition, we found that multi-predator effects varied at different predator-prey ratios. Thus, in total our results provide clear empirical evidence that, in this system, predator polycultures outperform monocultures over a broad range of predator densities and predator-prey ratios.

Introduction

The mechanisms responsible for greater prey consumption by multi- than single-species predator communities have been difficult to convincingly demonstrate. Few studies have reported clear evidence that a particular mechanism is at work (but see Bracken and Stachowicz 2006, Finke and Snyder 2008, Griffin et al. 2008). Often, elucidating the specific mechanisms driving these diversity effects has not been possible (Connolly 1986, 1988, Jolliffe 2000, Hooper 2005). There are two main mechanisms thought to be responsible for increased prey consumption by diverse communities of natural enemies, complementarity and facilitation (Loreau and Hector 2001, Tilman 2001, Casula et al. 2006). Complementarity occurs when different predator species attack different subsets of the prey population (Schoener 1974, Loreau and Hector 2001, Tilman 2001, Casula et al. 2006). Facilitation occurs when one predator species indirectly improves the foraging success of a second predator species (Losey and Denno 1998, Sih 1998).

Most studies investigating the relationship between predator biodiversity and ecosystem function (i.e., prey suppression) use a substitutive design, wherein total predator densities are held constant across single and multi-species communities (e.g. Wilby et al. 2005, Byrnes 2006, Snyder et al. 2006, Snyder et al. 2008, Straub and Snyder 2008). This design is useful to assess the importance of diversity *per se,* by eliminating any confounding effects of differing predator density across diversity levels (Straub and Snyder 2006a). However, within substitutive designs the density of conspecific predators decreases at higher levels of species richness. Thus, within a substitutive design high per capita consumption rates within diverse communities may simply reflect the relaxation of intraspecific competition. This phenomenon has not received as much

attention as a mechanism underlying emergent diversity effects as have complementarity and facilitation, but is an additional route through which diverse communities may outperform species-poor communities.

In the work reported here, in the field we simultaneously manipulated diversity and density among a community of aphid predators using a response-surface design, and measured resulting impacts on densities of two aphid species. Nested within our response-surface design were a series of substitutive manipulations of species richness, at varying total predator densities (Table 1). Response-surface designs sacrifice replication of particular treatment combinations for knowledge of effects across a broader range of treatment levels (predator densities in this case; Inouye 2001; Gotelli & Ellison 2004), and can be constructed, as was ours, to include multiple levels of substitutive manipulations within a single experiment (Sih et al. 1998; Griffiths et al. 2008). This allowed us to learn more about underlying causes of diversity effects in our system and their relationship to consumer-resource ratios.

Some insight into mechanism can be gained from analysis from our experiment. When analyzing the data using a substitutive design a significant predator diversity by density interaction would indicate that predators are partitioning resources, or released from intra-specific interference, but not facilitating one another. Complementarity is implicated because at higher densities of predators (above a certain threshold), predator monocultures will fully exploit their species-specific resource niche and therefore plateau in their ability to suppress aphids. In contrast, diverse communities that span several different resource-use will be more difficult to saturate, and aphid densities will plateau only at higher total predator densities and at lower overall densities of aphids. However, our experiment will not allow us to distinguish between niche partitioning and a release from intra specific competition. This is because if intra-specific

interference is strong, this could also generate the resource-use patterns for simple and diverse communities described above.

METHODS

Natural history

The experiments reported here were conducted within a well-studied community of insect predators common on *Brassica oleracea* plants in Washington, USA, infested with the aphids *Myzus persicae* and *Brevicoryne brassicae*. In this community, overall consumption of aphid herbivores dramatically increases when more predator species are present (Snyder et al. 2006; Snyder et al. 2008; Straub & Snyder 2008). Dominant predator species in the system include the sit-and-wait predatory bug *Nabis alternatus*, the actively searching predatory lady beetles *Hippodamia convergens* and *Coccinella septempunctata*, and the endoparasitoid wasp *Diaeretiella rapae* (Snyder et al. 2006). In addition to differences in hunting style, the predators encompass a broad range of body sizes and tend to forage in different locations on the plant (Straub & Snyder 2006; 2008). Differences along each of these three trait axes have been proposed to foster complementary effects on shared prey, and thus a positive relationship between diversity and prey consumption (Ives et al. 2005; Wilby et al. 2005; Casula et al. 2006; Schmitz 2007

Experimental design

Our experimental units were 2 × 2 × 2-m field cages, covered with fine mesh and constructed as previously described (Snyder et al. 2006). Each cage enclosed 8 aphid-infested *B. olearacea* plants. We manipulated predators within a response-surface design, to achieve a fully-factorial cross of consumer diversity (each of the four predator species in separate monocultures, versus a diverse mix of all four species) and total consumer density (0, 2, 4, 8, 16 or 32 predators per cage) (Table 1). These predator densities approximated 0, 0.25, 0.5, 1, 2 and 4× local mean open-field density of these predators on *B. oleracea* plants that year (S. Steffan, T. Northfield, G. Snyder and W. E. Snyder, unpublished data). Thus, the full experimental design included 25 unique treatment combinations (Table 1). The experiment was repeated twice, with 2 replicates (no predator controls included 3 replicates in Trial 1 and 5 replicates in Trial 2). This experiment was itself repeated, for a total of 104 total replicate arenas across the two trials.

Methodological details of the field experiment

The experiments were conducted at the Washington State University research station in Othello, WA. Trial 1 was initiated on 20 June, and Trial 2 on 25 July, 2007. Each cage housed 8, 4-week-old *B. oleracea* plants, transplanted from the greenhouse (as in Snyder et al. 2006). Aphids were released onto plants 24 h after the collards were transplanted. In Trial 1, 10 aphids per species per plant were released (i.e., 80 aphids per species and 160 aphids total, per cage). In Trial 2, anticipating more rapid aphid population growth typical of mid-summer, and seeking to achieve similar aphid densities to Trial 1, 5 aphids per species per plant (i.e., 40 aphids per species and 80 aphids total, per cage) were released. The aphids were reared on *B. oleracea* plants in field cages prior to the experiments. For both trials, aphids were allowed to acclimate to the plants for

24 h, after which their densities were censused by counting all aphids on 4 randomly selected plants per cage. These data were initially included as a covariate but were dropped from the analyses as they were never statistically significant.

After the initial aphid count, predators were released into each cage with density and species composition determined by treatment (Table 1). True predators were collected from surrounding vegetation using a D-vac suction sampler, sexed, and released into cages to establish an even (1:1 male-female) sex ratio for all species. All predators were adults and were starved 24 hours prior to release into field cages. The parasitoid *D. rapae* was reared in field cages, using both aphid species on *B. oleracea* plants. Four weeks after predator release, aphids were again sampled by counting all aphids and predators on 4 randomly-selected plants per cage. At this time parasitoids were in their second generation and at the pupal stage. At this pupal stage the host aphid's exoskeleton has a distinctive, bloated and papery appearance, called the mummy, which is easily counted. The experiment was then terminated by destructively sampling four plants in each cage and hand-collecting predators. The length of the experiments allowed for true predator reproduction to occur, and for some young produced *in situ* to nearly reach the adult stage (Snyder et al. 2006).

Data Analysis

Predator diversity/density effects on prey consumption

We performed three separate 3-way ANOVAs, all with temporal block as the third factor. We examined whether predators reduced aphid densities by comparing total aphid densities in cages containing predators (pooled low and high predator diversity treatments) to those in the no predator controls, at each level of predator density (0, 4, 8, 16, and 32). We tested the hypothesis

that predator diversity effects on aphid suppression changed with predator density by using a factorial cross of predator diversity (low versus high) and predator density (4, 8, 16, and 32). To assess predator density dynamics we compared final per-capita recovery of predators and parasitoids (number of individuals collected at the last sample divided by the initial density) in low and high predator diversity at each predator density. All initial analyses included pre-predator release aphid counts as a covariate, but covariates were dropped from the analysis due to non-significance .

Results

Predator diversity/density effects on prey consumption

Total aphid densities were significantly lower in the presence of predators, compared to the no-predator controls ($F_{4,78} = 4.823$, $P = 0.002$). The block main effect was also significant ($F_{1,78} = 72.375$, $P < 0.0001$), but the block by predator density interaction was not ($F_{4,78} = 0.362$, $P = 0.835$).

Looking again at aphids densities, in the factorial cross of predator diversity (low versus high) and predator density (4, 8, 16, and 32), with 2 temporal blocks, we found that the 3-way interaction among predator diversity, density, and block was not significant ($F_{3, 64} = 0.308$, $P = 0.819$), nor was there a significant 2-way interaction between predator density and block ($F_{3, 64} = 0.160$, $P = 0.923$). However, The 2-way predator diversity by block interaction was significant ($F_{1, 64} = 4.126$, $P = 0.046$), with monoculture and polyculture treatments diverging at lower predator densities in Block 2 than Block 1. The predator diversity by predator density interactive effect was also significant ($F_{3, 64} = 3.570$, $P = 0.019$); the magnitude of increased prey

consumption in diverse communities increased concomitantly with predator density. Main effects for block, predator diversity, and total predator density were significant ($F_{1, 64}$= 116.109, $P < 0.001$, $F_{1, 64}$= 38.713, $P < 0.001$, $F_{3, 64}$= 5.899, $P = 0.001$, respectively) (Table 2, Fig. 1 a and b).

Effects on predators

True predator reproduction was common in the first trial (early summer) when predator reproduction was maximal (e.g., Snyder et al. 2006). Thus, predator densities generally exceeded the number initially added [Fig. 2(a)]. However, true predator reproduction rarely occurred in the second trial, conducted well into the summer drought typical for the region, and thus at a time when activity of most predators naturally declined. Thus, predator densities declined over the course of the second trial (Fig. 2 c). Per capita predator recovery at the end of Trial 1 generally decreased with increasing predator density, but predator density, predator diversity, or their interaction did not significantly impact predator densities in either trial (Table 3). As with true predators, per capita parasitoid reproduction was higher in Trial 1 than Trial 2 [Fig. 2(b, d); Table 4]. However, parasitoid densities were not significantly impacted by predator diversity or density, or their interactions, in either trial [Table 4].

Discussion

All aphid density ANOVA blocking effects were significant, because trial 1 cages were seeded with twice the number of aphids as Trial 2. This significant difference in aphid densities between

trials one and two allowed us to not only investigate the effects of varying overall predator densities and diversity, but also extended the range of predator-prey ratios manipulated in these two trials. In the 3-way ANOVA, which included predator diversity, predator density and trial as factors, there was a significant block by predator diversity interaction indicating a different trend for aphid consumption in diverse versus single species treatments in the two blocks (Fig. 1 a and b, Table 2). This would be expected with complementarity, as the effect of complementarity in a substitutive design can be detected more readily when resources are limiting (Wilby 2005, Weis et al. 2007). Resources were relatively more limiting in trial one at the lowest predator densities than in trial two at the lower predator densities, as there were significantly more aphids and thus a lower predator-prey ratio in trial 1. These findings are consistent with the two other recent studies that manipulated both predator diversity and density, and found that predator diversity effects that were strong at high predator densities but attenuated when densities were lower (Griffin et al. 2008, Griffiths et al. 2008).

In our studies there was also a significant predator diversity by predator density interaction, reflecting increasing divergence between low and high diversity treatments with increasing predator density (Fig. 1 a, b). This suggests that species could be partitioning resources. With resource partitioning, any single species will rapidly deplete the subset of the prey population that is subject to its attack, with niche saturation occurring at relatively low predator density and relatively high abundance of the prey resource. In contrast, for a diverse predator community depletion of available prey occurs only at higher predator densities, because it takes more individuals to fully exploit the broader range of resources available to several different species. The significant predator diversity by predator density interaction could also

occur with a release from intraspecific interactions in the diverse community assemblages, but it would not be expected to occur with predator-predator facilitation.

In order to create policies that preserve ecosystem function, researchers have focused on experimental designs that test specific mechanisms driving positive diversity effects (Yachi and Loreau 2007). But, perhaps when we lack the ability to distinguish between even the more general processes responsible for the positive effects of diversity, a focus on specific mechanisms is misplaced. Instead, our focus should be on determining whether organisms are able to increase ecosystem function in diverse communities because they are able to partition resources, are released from negative conspecific interactions, or have emergent synergistic impacts. The methodology used in this experiment allowed us to infer that the predators in this system are likely released from negative conspecific interactions that drove the positive effect of diversity rather than facilitation.

In my work, in trial one at lower predator-prey ratios there was no detectable effect of diversity on prey consumption. However, diversity effects grew increasingly strong at higher predator densities. BEF studies that use a substitutive design generally include one arbitrary predator-prey ratio (Inouye 2001). If that ratio is lower than what would be found in a natural system the investigator may wrongly conclude that greater predator diversity does not increase prey consumption. Conversely, if investigators use a predator prey ratio well beyond any found in nature they might wrongly conclude that greater predator diversity consistently strengthens prey suppression. Thus we believe the methodology used here should be applied to all BEF predator-prey studies looking for a general pattern in increasing predator diversity and pest suppression. Testing diversity over a range of predator densities is also more representative of

natural systems where predator-prey ratios are likely fluid and change throughout the growing season.

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Table 1. The treatment structure for the two field experiments (Trials 1 and 2). Predator diversity (1 or 4 species) was manipulated across six levels of predator density (0, 2, 4, 8, 16, or 32 individuals per cage). This resulted in 25 unique treatment combinations, each of which was replicated twice in each of 2 temporal blocks. Each row constitutes a substitutive design (different combinations of predators at the same density).

	Predator species composition					
	Ø	*Coccinella*	*Diaeretiella*	*Hippodamia*	*Nabis*	Diverse (4 spp.)
	0	2	2	2	2	
Predator		4	4	4	4	$1 + 1 + 1 + 1 = 4$
density		8	8	8	8	$2 + 2 + 2 + 2 = 8$
		16	16	16	16	$4 + 4 + 4 + 4 = 16$
		32	32	32	32	$8 + 8 + 8 + 8 = 32$

Table 2. Three-way ANOVA including predator diversity (monoculture, polyculture), predator density (4, 8, 16 and 32) and two temporal blocks as factors with final aphid counts (log 10) as response variable.

Model Terms	df	F-ratio	P
Predator diversity (monoculture or polyculture)	1	38.713	0.000
Predator density (4, 8, 16, or 32 total predators)	3	5.899	0.001
Block (2 temporal blocks)	1	116.109	0.000
Predator diversity x Predator density	3	3.570	0.019
Predator diversity x Block	1	4.126	0.046
Predator density x Block	3	0.160	0.923
Predator diversity x Predator density x Block	3	0.308	0.819

Table 3. Three-way ANOVA for the proportion of true predators recovered at the end of the experiment. The effects of Diversity (1 versus 4 species), Predator Density (4,8,16,32), and Block (2 temporal blocks) are fully crossed.

Source	d.f.	MS	*F-ratio*	*P*
Diversity	1	3.329	0.081	0.778
Predator Density	3	87.697	2.123	0.110
Block	1	352.676	8.539	0.005
Diversity × Predator Density	3	9.047	0.219	0.883
Diversity × Block	1	3.806	0.092	0.763
Predator Density × Block	3	87.323	2.114	0.111
Diversity × Predator Density × Block	3	7.969	0.193	0.901
Error	48	41.3		

Table 4 Three-way ANOVA proportion of parasitoids recovered at the end of the experiment. The effects of Diversity (1 versus 4 species), Parasitoid Density (4,8,16, and 32), and Block (2 temporal blocks) are fully crossed.

Source	d.f.	MS	*F-ratio*	*P*
Diversity	1	0.073	0.005	0.946
Parasitoid Density	3	7.511	.490	0.695
Block	1	183.659	11.971	0.004
Diversity × Parasitoid Density	3	20.056	1.307	0.311
Diversity × Block	1	1.242	0.081	0.780
Parasitoid Density × Block	3	7.143	0.466	0.711
Diversity × Predator Density × Block	3	19.784	1.289	0.317
Error	14	15.342		

Figure 1 Log 10 transformed mean total aphid density for single species treatment (mono) and all predator species together (poly): at total predator densities (0,2,4,8,16 and 32), in experimental trials 1 (a) and 2 (b). Error bars represent means ± 1SE. Scales on the y axis are different for each block

a. Block one

b. Block two

Total predator density

Log aphid/plant

Mono
Poly
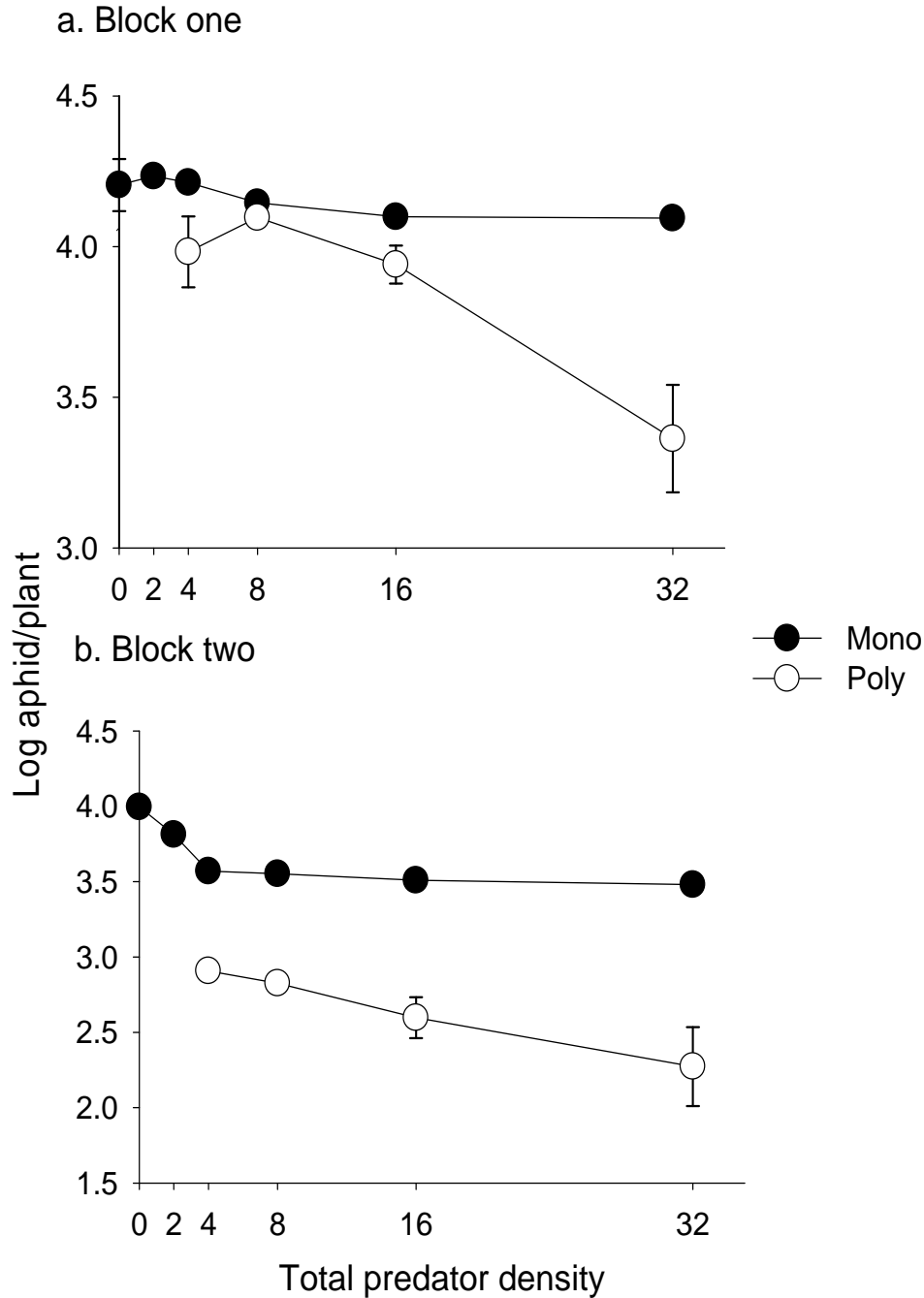
Figure 2 Natural enemies recovered at the end of the experiment, divided by the number originally released, summed for true predators in (a) Block 1 and (c) Block 2, and for pupae of the parasitoid *D. rapae* in (b) Block 1 and (d) Block 2. Error bars represent means ± 1 s.e.
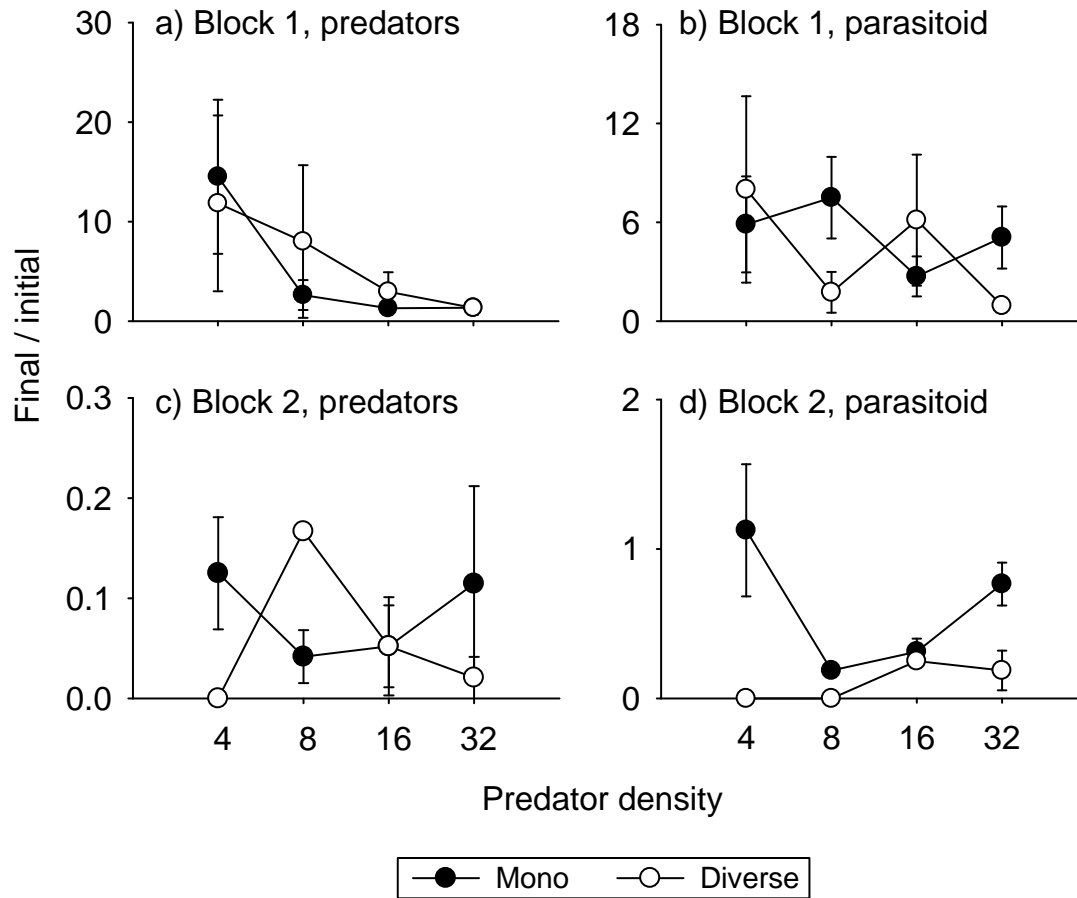
Conclusions of This Dissertation

The objective of this dissertation was to gain a better understanding of the mechanisms contributing to improved herbivore suppression with greater predator biodiversity, for the community of predominant predators and the predominant parasitoid attacking aphids on collards.

In the experiments presented in Chapter 2 we determined that stronger aphid suppression with greater predator diversity was independent of prey species identity or diversity. There are many ways in which predators can increase consumption in diverse communities and it is not logistically possible to test all of them. For instance, if multiple predator species are complementary because they partition resources they could do so along many niche dimensions. These include but are not limited to differing foraging strategies (Ives et al. 2005), spatial foraging differences (Straub and Snyder 2008), and predators could partitioning resources temporally as well. Predator interactions could also be synergistic if shared prey are more vulnerable to predation by multiple than any single predator species because of behavioral effects on predators, prey or both. Lastly, combinations of predator species could be more effective than individual species at the same densities if interspecific interference is greater than intraspecific interference. These broad categories of potential effects should be distinguishable based on effects of various combinations of predators on prey suppression and this was the approach I followed in my studies. The results of such experiments can guide subsequent research to delineate precise mechanisms.

In 2007 we conducted an experiment designed to detect general mechanisms for the positive effect of predator diversity. Here we found that it was likely a release from intra-specific interactions driving the positive effect of diversity in our system (Chapter 3). The results of this

study can direct future experiments to determine either how predators can partition resources or what type of negative interactions between conspecific contribute to this effect. For instance it is possible that predators release chemical cues that cause conspecific predators to visit plants to forage less often with conspecific than heterospecifics (e.g Doumbia et al. 1998, Rutledge et al. 2008). In addition, the study presented in Chapter 3 demonstrates the importance of predator density in biodiversity and ecosystem function studies. Two points of interest stand out in light of these findings. One is that if empirical studies use substitutive designs and do not find a positive effect of diversity it is possible they are using a predator-prey ratio that is too high to detect the effect of diversity. Thus, to measure whether predator diversity determines ecosystem function predators and prey density manipulations should represent ambient densities. Also, the confounding of predator-prey ratio with predator diversity, as occurs in an additive design, is very likely misleading. A response surface design is likely the strongest for BEF studies, especially those testing the effects of diversity on prey consumption. Secondly, if intraspecific interactions are largely responsible for increased prey suppression by diverse communities, such as was evidently true in our work, there is a real need to consider the evenness of predator abundance into BEF studies.

Almost all previous studies designed to isolate emergent predator diversity effects in high species richness treatments included predators in a one-to-one ratio in polyculture. This ratio is atypical of predator to predator ratios in nature; perhaps diversity studies more representative of natural systems will generate results that can improve extrapolation of the consequences of diversity loss in manipulative experiments to the real-world agricultural setting. For example, including real-world predator densities could modify the effects of diversity, especially if natural predator densities reflect a natural equilibrium. For example, *Nabis* and *Geocoris* (in our system)

might be able to exist at higher densities than the other predators because they experience less intraspecific competition and/or are able to sustain higher densities with fewer resource than can larger predators. If this is true then we would expect that when the rank abundance order and ratios of predators found in open fields are incorporated into the high diversity treatments, the effect of diversity will be heightened. Increasing the density of a predator that experiences weaker intraspecific competition in the high diversity treatment should not interfere with its ability to suppress prey. Similarly, decreasing the density of a predator that experiences stronger intra- than interspecific competition in the high diversity treatment should increase its per capita consumption. Of course, this is one of many possible scenarios, but it highlights the need for more work in this area. Indeed one recent study that manipulated the richness and evenness of bacteria in microbial microcosm found that initial evenness strongly influenced resistance of communities to an environmental stress. Future studies should incorporate realistic predator-prey ratios and predator evenness into predator-prey BEF studies, in order to understand how predator diversity affects prey suppression under field conditions.

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