

EXPLORING THE RELATIONSHIP BETWEEN NATURAL ENEMY
BIODIVERSITY AND HERBIVORE SUPPRESSION

By

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Chair

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Abstract

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Agricultural pest suppression is a valuable ecosystem service that may be enhanced by the conservation of natural enemy species. However, it is unclear how conserving natural enemy diversity *per se* affects the biological control of pests, because few studies have attempted to distinguish between the effects of enemy abundance, identity, composition, and diversity. In chapter 1, I discuss how an experimental approach traditionally used in plant studies can be adapted to isolate the effects of enemy diversity on the suppression of herbivores. In chapter 2, I apply this experimental approach to examine how increasing enemy diversity within the potato agroecosystem affects the biological control of the green peach aphid, *Myzus persicae*. In this study, I find that increasing enemy diversity has no overall effect on the strength of aphid suppression. In chapter 3, I focus on a different assemblage of enemy species, one in which interference may be particularly likely, and examine how both the diversity and composition of the enemy community affect the strength of biological control. I find that increasing enemy diversity can strengthen, weaken, or not affect the suppression of herbivores, depending

on the particular composition of enemy species that coexist in the community. In chapter 4 I test the hypothesis that multi-enemy effects on prey suppression may also vary with the identity of the plant species upon which the higher trophic levels interact. Here I focus on a single composition of enemy species that occurs in both potato and collard agroecosystems. I find that increasing diversity within this enemy assemblage leads to stronger aphid suppression on both plant species. However, because aphids reproduced at a much higher rate on collards than on potatoes, increasing enemy diversity reduced aphid populations by ~ 200 aphids per plant on collards but only by ~ 6 aphids per plant on potatoes. This indicates that the value of conserving enemy diversity will be far greater on collards than on potatoes. Taken together, this body research shows that a general relationship between enemy diversity and biological control may not exist, and that the value of conserving enemy diversity *per se* will likely vary among agroecosystems.

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CHAPTER 1

INTRODUCTION

EXPERIMENTAL APPROACHES TO UNDERSTANDING THE RELATIONSHIP BETWEEN PREDATOR BIODIVERSITY AND BIOLOGICAL CONTROL

Abstract. Conservation biological control (CBC) involves the manipulation of the environment to favour the natural enemies of pests. Alternative agricultural practices, such as organic farming, are more biodiversity-friendly than conventional agricultural practices and generally lead to greater predator species richness and abundance. This is desirable from a conservation perspective, but it is unclear how greater predator diversity affects biological control. Unfortunately, the predator ecology literature provides little guidance: increasing the number of predator species has been shown to enhance, diminish, and not affect prey suppression. In this chapter we explore how the experimental approach used in biodiversity and ecosystem functioning (BEF) studies, which focus on the ecological consequences of species loss, may be used to study how increasing predator diversity affects biological control. The notable features of this approach are: 1) realistic levels of species richness (i.e., > 2 predator species), 2) the use of substitutive, rather than additive, experimental designs, and 3) experimentally distinguishing the effect of species richness from the effects of species abundance, composition, and identity. This experimental approach can be used to identify which components of predator biodiversity—species richness, abundance, composition, and identity—should be targeted by CBC practitioners to maximize pest suppression. Further, it can be used to assess whether predator biodiversity conservation and biological control

are truly compatible goals. Ultimately, we hope that this chapter will serve to motivate future research into this important problem.

1. INTRODUCTION

Conservation biological control (CBC) involves the manipulation of the environment to favour the natural enemies of pests (Barbosa 1998). This may be achieved by removing deleterious factors, such as broad spectrum pesticides, and by providing limiting resources that natural enemies need to survive and flourish in agroecosystems. CBC is appealing because it can be implemented directly by growers and because it is a potentially sustainable pest management practice (Barbosa 1998).

While the primary goal of CBC is to control pests by enhancing naturally occurring predator populations, CBC serves the additional function of conserving predator species, which are generally more vulnerable to extinction than lower-trophic level species (Kruess and Tscharntke 1994, Duffy 2002). The conservation component of CBC is particularly relevant given that modern agriculture is predicted to threaten biodiversity on a scale that rivals global warming (Tilman et al. 2001). Alternative agricultural practices, such as organic farming, are widely believed to be more biodiversity friendly and may thus be an important strategy for mitigating this biodiversity loss (Krebs et al. 1999, DEFRA 2002, EU 2002). Numerous studies have compared biodiversity on conventional and organic farms to test the assertion that biodiversity is conserved by organic agriculture. A recent review of these studies (Hole et al. 2005) and a meta-analysis (Bengtsson et al. 2005) found that biodiversity is enhanced by organic management practices. For predatory arthropods in particular, the

meta-analysis showed that both species richness and abundance increases with organic management (Bengtsson et al. 2005). Ground beetles (Carabidae) also showed greater species richness and abundance on organic compared with conventional farms. Carabids were excluded from the predatory arthropod category but are often predacious (Ball and Bousquet 2001), suggesting that the benefit of organic management to predator biodiversity is even more pronounced. One explanation for why organic agriculture promotes greater predator diversity is that there is less reliance on persistent, broad-spectrum pesticides. As these pesticides continue to fall out of favour because of the risks of non-target effects (EPA 2003), it seems likely that predator diversity will also be on the rise in conventional agroecosystems.

Greater predator biodiversity on farms is clearly desirable from a conservation perspective, but its consequences for pest suppression are less clear (Snyder et al. 2005). This is because the conserved predators are often generalists. While generalist predators can be effective biological control agents (Chang and Kareiva 1999, Symondson et al. 2002), they may not reliably improve pest suppression because they also eat non-pest prey, including other predators (Polis et al. 1989, Rosenheim et al. 1995). Such food-web complexity may make the top-down control of prey populations unlikely (Strong 1992, Polis and Strong 1996). Indeed, adding intraguild predators to experimental communities has been shown to disrupt herbivore suppression (Rosenheim et al. 1993, Snyder and Ives 2001, see also Rosenheim and Harmon, this volume, who present a meta-analysis of the role of intraguild predators in biological control) and dampen trophic cascades (Snyder and Wise 2001, Finke and Denno 2004). However, agroecologists have often suggested that greater species richness should generally improve pest suppression (Pimentel 1961,

Altieri 1994, Kruess and Tscharnkte 2000). There is some experimental evidence for this view as well (Cardinale et al. 2003, Aquilino et al. 2005, Björkman and Liman 2005). In addition to the positive and negative effects of predator diversity, several studies have found no effect of increasing predator species richness on herbivore suppression (Evans 1991, Chang 1996, Rodriguez and Hawkins 2000, Schmitz and Sokol-Hessner 2002, Vance-Chalcraft et al. 2004, Aukema and Raffa 2004, Straub and Snyder 2006). Thus, the predator ecology literature provides conflicting views on the value of predator biodiversity to biological control.

The uncertain relationship between predator biodiversity and biological control presents an important problem for agriculture and the environment. Organic growers have fewer chemical pest control options and more predator species than conventional growers. Thus, whether increasing predator biodiversity strengthens, weakens, or does not affect biological control will at least partially determine the extent to which growers find it profitable to adopt organic agricultural practices. This, in turn, will determine the extent to which agriculture continues to threaten biodiversity. Finke and Denno (2004) recently brought attention to this problem by questioning whether biodiversity conservation and biological control are compatible goals. In this essay we explore how CBC researchers can address this problem by adapting an experimental approach developed by ecosystem ecologists.

2. Biodiversity and ecosystem functioning (BEF) and multiple-predator studies

Two lines of research, biodiversity and ecosystem functioning (BEF) and multiple-predator studies, are relevant to our understanding of the relationship between

predator biodiversity and biological control. It has recently been appreciated that an exchange of ideas among these historically distinct sub-disciplines can lead to valuable insights (Wilby and Thomas 2002a, Wilby and Thomas 2002b, Ives et al. 2005). We believe this to be particularly true in the case of CBC, where the uncertain consequence of increasing predator diversity has emerged as a problem of paramount importance. Here we examine the approaches, objectives, and experimental designs of BEF and multiple-predator studies, pointing out their similarities and differences.

2.1. Approaches and objectives of BEF and multiple-predator studies

Interest in the relationship between biodiversity and ecosystem functioning has been motivated by alarming declines in global biodiversity (Kinzig et al. 2002, Loreau et al. 2002). Ecosystem functioning refers to ecological processes such as primary production, decomposition, pollination, and natural pest suppression. Many of these ecosystem functions directly impact human welfare, and the concern is that ecosystems will lose the ability provide these valuable services as species are lost. Early studies focused on plant communities (e.g., Tilman et al. 1997) and sought to distinguish between alternative hypotheses describing the relationship between biodiversity and ecosystem functioning. These hypotheses are presented graphically in Figure 1a, and are extended to the relationship between predator biodiversity and biological control in Figure 1b. The final point on the x-axis represents communities with the full complement of naturally occurring diversity, the first point represents communities with no species, and the trajectory of the line connecting these points represents how ecosystem functioning (or biological control) is hypothesized to change as diversity is

lost. To test these hypotheses, BEF studies start with high levels of diversity and experimentally subtract species to mimic extinction. We refer to this as a top-down approach. By contrast, multiple-predator studies have used what we will call a bottom-up approach. These studies often start with a focal predator-prey interaction and add predator species to see how (or if) the focal interaction is modified. Because more species are included in BEF studies than in multiple-predator studies, the species interactions that give rise to the observed patterns are more tractable in the latter. This represents a difference in the objectives of BEF and multiple-predator studies—the former have emphasized pattern (Fig. 1) and the latter process.

While BEF studies generally include numerous species and have emphasized pattern over process, they have evolved from more process-oriented studies. These earlier studies typically focused on competition within and between plant species. Such plant competition studies are particularly common in the intercropping literature, where the objective has been to identify species combinations that maximize primary productivity (Vandermeer 1989). These studies look to see if combining plant species leads tooveryielding, or greater primary productivity in species mixtures than is expected from the performance of each of the constituent species in monoculture (e.g., Petchey 2003). When this emergent effect is observed, the interacting species are described as complementary. Species complementarity can occur through resource partitioning, when plant species use resources in different ways and combine to use more resources than any one species could by itself, or through facilitation, when one plant species increases the consumption rate and growth of a second species (Loreau et al. 2001). As plant ecologists began to explore more complex communities in BEF studies, they were able to make

inferences about the underlying species interactions based on knowledge gained from the earlier plant competition studies. For example, many BEF studies have measured primary productivity, an important ecosystem property, and used overyielding to infer complementarity among species in diverse assemblages.

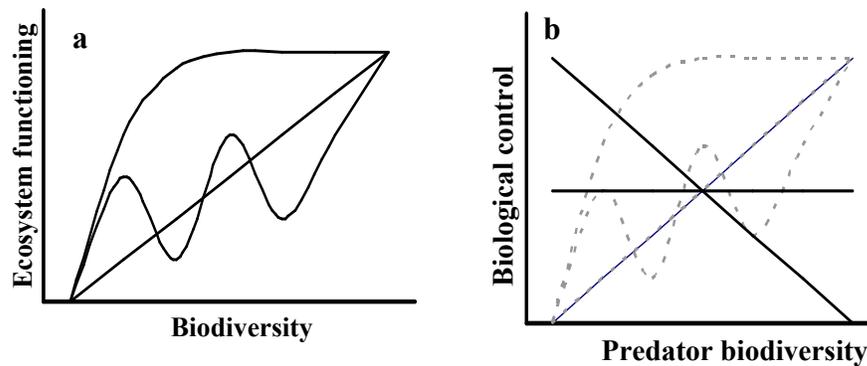


Figure 1. a, Hypothesized relationships between biodiversity and ecosystem functioning. From left to right, biodiversity ranges from 0 species to the natural level of biodiversity. The redundancy hypothesis (the line that increases and then levels off) states that ecosystem functioning increases with biodiversity until a point at which additional species have no additional effect. This hypothesis implies that species occupy several functional roles, but that most species are functionally identical and thus redundant. The linear hypothesis (the straight line) states that ecosystem functioning increases with biodiversity in a linear fashion. This hypothesis implies that species are functionally unique and have positive, but equivalent, effects. The idiosyncratic hypothesis (the wavy line) states that ecosystem functioning changes with biodiversity in an idiosyncratic fashion. This hypothesis implies that species are unique and have positive and negative effects that vary in magnitude. b, Hypotheses about the relationship between biodiversity and ecosystem functioning can be extended to the relationship between predator biodiversity and biological control. The predator ecology literature suggests two additional relationships: no relationship, and a negative (but not necessarily linear) relationship between predator biodiversity and biological control.

The goal of multiple-predator studies has also been to identify the emergent effects of combining species. Here the response variable of interest is prey population size (rather than biomass). Emergent effects are observed when the prey population size differs from that predicted by summing the impacts of each predator species when in

monoculture (Sih et al. 1998). Emergent predator impacts may be positive, such that multiple predators suppress prey to a greater extent than predicted from their individual impacts, or negative, such that prey suppression is less than that predicted by summing individual predator impacts. Positive emergent impacts are called synergism, facilitation, or prey risk enhancement, and negative emergent impacts are called antagonism or prey risk reduction (Sih et al. 1998). When the impact of multiple predators does not differ from expectations based on individual predator impacts, there is no evidence for predator-predator interaction and the combined impact is additive (Sih et al. 1998). Most ecologists would likely agree that predator-predator interactions and their consequences for prey suppression are well understood. Thus, like the plant ecologists who pioneered the field of BEF, it seems that predator ecologists are now well prepared to investigate more complicated consumer communities. As we discuss in the next section, predator ecologists will want to carefully choose their experimental design.

2.2. Experimental designs used by BEF and multiple-predator studies

One important difference between BEF and multiple-predator studies is that workers in these sub-disciplines have typically employed different experimental designs. BEF researchers have generally used substitutive, or replacement series designs, while multiple-predator studies have typically used additive series designs. Here we argue that the substitutive design may be more appropriate for assessing the value of predator diversity per se, but acknowledge that this approach also has its limitations.

2.2.1. Substitutive versus additive designs

In substitutive experimental designs, species richness is manipulated but the total abundance (or initial biomass) of individuals is held constant across richness treatments. To hold the total abundance of individuals constant, intraspecific densities are systematically reduced at increasing levels of richness (Connolly 1998, Jolliffe 2000). Thus, as species richness increases, the opportunity for intraspecific interactions decreases, while the opportunity for interspecific interactions increases. This approach allows a direct comparison of communities dominated by intra- versus interspecific interactions. In essence, the substitutive design tests the simple hypothesis that competition (and interference) is greater among conspecifics than among heterospecifics. This is expected if different species utilize different resources. If this hypothesis is supported, then conserving species richness (i.e., adding new species to a community) will lead to greater total resource exploitation than conserving abundance (i.e., adding more individuals of the species that already exist in the community). In the case of plant communities this is manifested as greater primary productivity (an ecosystem property); in the case of predator communities it is manifested as greater herbivore suppression (an ecosystem process and an important service in the context of agriculture).

While BEF researchers directly compare communities dominated by intra- and interspecific interactions, ecologists interested in multiple-predator effects typically focus on how interspecific interactions among predators affect prey populations. Thus, they hold intraspecific densities constant across levels of species richness in an attempt to isolate the effect of interspecific interactions. As a consequence, the total density of predators increases with species richness. The advantage of this additive experimental design is that it can be analyzed by a factorial ANOVA, and significant interaction terms

can be used to identify the emergent effects of predators on their prey. However, these emergent effects may be caused by increasing species richness, by increasing the total abundance of predators, or by both factors. Importantly, synergism and antagonism are not restricted to interspecific interactions--adding more of the same species can lead to these emergent effects, just as adding different species can. Sih et al. (1998) note that this problem may be particularly acute in the case of antagonism. This is because increasing the density of single predator species generally leads to a decline in its per-capita effect on prey, a phenomenon known as predator interference. If there is no difference in the strength of intra- and interspecific interference, it is incorrect to conclude that antagonism is an emergent effect of increasing species richness (Sih et al. 1998). Thus, substitutive designs, which hold the total abundance of predators constant and directly compare the strength of intra- and interspecific interference, may be more appropriate for assessing the effect of increasing predator species richness. While we are only aware of a few multiple-predator studies that have used the substitutive design (Evans 1991, Chang 1996, White and Eigenbrode 2000, Schmitz and Sokol-Hessner 2002, Vance-Chalcraft et al. 2004, Aquilino et al. 2005, Björkman and Liman 2005, Straub and Snyder 2006), it is interesting to note that none of these studies have found that predator interference increases with species richness.

From our perspective, a clear objective of CBC programs should be to conserve predator abundance, because there is little doubt that increasing the total abundance of predators will generally improve biological control. However, predator interference (both intra- and interspecific) will almost always place limits on the benefits of increasing abundance. If adding new predator species leads to less interference, and a greater per-

capita impact, than adding more of the same species, then there may also be value in conserving predator species richness. It is only through careful experimentation that CBC researchers can determine if, in addition to predator abundance, predator species richness itself should be targeted for conservation. Because additive experimental designs compound the effects of intra- and interspecific interference, while substitutive designs directly compare them, we believe the latter to be more appropriate for assessing whether greater predator species richness is good, bad, or neutral for biological control.

2.2.2. Limitations of the substitutive design

As with any experimental approach, the substitutive design also has its limitations. The primary problem is that, to hold the total abundance of individuals constant, the density of each species is systematically reduced at increasing levels of species richness. This can lead to confusion in the interpretation of the experimental results (Connolly 1998, Jolliffe 2000). For example, if herbivore suppression is strengthened by increasing predator species richness in a substitutive design (e.g., White and Eigenbrode 2000, Aquilino et al. 2005, Björkman and Liman 2005), the underlying mechanism may be a release from intraspecific interference--if some predators have a greater per-capita impact in the presence of fewer conspecifics, then the richer communities will exert stronger top-down suppression despite having the same total number of individuals. However, stronger herbivore suppression in the more diverse communities may also be driven by facilitation among predator species, that is, it may be caused by interspecific interactions. And of course, both mechanisms may be operating simultaneously. Thus, substitutive designs do not readily reveal the mechanisms driving

differences between levels of species richness. This reiterates our earlier statement that BEF studies have emphasized pattern over process.

A potentially fruitful approach might be to follow the substitutive experiment with an additive experiment. Having answered our first research question—in our example, increasing species richness improves biological control—we can use an additive design to test for antagonism, additivity, or facilitation. Both antagonism and additivity would suggest that, even if interspecific interference also occurs (in the case of antagonism), it was a release from intraspecific interference that led to greater biocontrol in the substitutive experiment. This result suggests that strong negative interactions among conspecifics places a limit on their ability to suppress pests, and new species must be added to suppress herbivore populations to a lower level. By contrast, facilitation would indicate that at least some of the predator species became more effective because of greater species richness. This latter outcome provides the most compelling reason to conserve predator species richness. Thus, if interpreted appropriately, additive experimental designs may complement substitutive designs by improving our understanding of how predator biodiversity affects biological control (Ives et al. 2005).

A second potential criticism of substitutive designs is that they do not accurately mimic changes in predator biodiversity because, while substitutive designs uncouple predator species richness and total predator abundance, these factors are often positively correlated in the field (Cardinale et al. 2003, Bengtsson et al. 2005, Finke and Denno 2005, Hole et al. 2005). Additive experimental designs avoid this problem by increasing both predator species richness and total predator abundance in the high diversity treatment. However, additive designs may also fail to accurately mimic changes in

predator biodiversity because, while predator and prey abundance are often positively correlated in the field (Cardinale et al. 2003, Koss et al. 2005), additive designs increase predator abundance in the high diversity treatment but hold the total prey density constant across levels of diversity. Thus, by increasing the total predator abundance in the high diversity treatment, additive designs successfully mimic the natural correlation between predator richness and abundance but may fail to capture the natural correlation between predator and prey abundance. Conversely, by holding predator abundance constant across levels of diversity, the substitutive design fails to capture the natural correlation between predator richness and total predator abundance but may successfully mimic the natural correlation between predator and prey abundance (Straub and Snyder 2006). One solution to this apparent trade-off might be to increase both predator and prey abundance in high diversity treatments. By combining the strengths of both substitutive and additive designs, this synthetic experimental approach may model changes in predator biodiversity more accurately.

3. Disentangling the components of predator biodiversity

To assess the compatibility of predator conservation and biological control, studies that isolate the effect of predator species richness on biocontrol are clearly needed. To improve CBC, studies will also have to evaluate the importance of predator abundance, composition and identity. These components of predator biodiversity--species richness, abundance, composition and identity--are often correlated in nature, and careful experimental designs are needed to tease apart their independent effects. Fortunately, BEF studies have made considerable progress on this front. As we hope to

demonstrate in this section, an exciting opportunity for experimental work in CBC awaits.

3.1. Species richness and abundance

Both predator species richness and abundance are increasing in response to organic management (Bengtsson et al. 2005). Each of these components of predator biodiversity can affect the strength of biological control. Because BEF studies have almost always used species richness as their metric of biodiversity, they have largely ignored the effects of abundance. Multiple-predator studies, by virtue of their heavy reliance on additive experimental designs, have usually manipulated both abundance and richness simultaneously. As mentioned above, this approach captures the natural correlation between increasing species richness and total predator abundance (Cardinale et al. 2003, Bengtsson et al. 2005, Finke and Denno 2005, Hole et al. 2005), but is unable to identify which component of predator biodiversity, if not both, should be conserved to maximize pest suppression.

Interestingly, by overlooking abundance effects, BEF researchers may have oversimplified an important concept in both ecosystem and predator ecology. This is the concept of functional redundancy. While any two species will often differ in many ways, they can be identical with respect to any one function, such as the suppression of a prey species (Sih et al. 1998, Chalcraft and Reserits 2003). A premise of much BEF work is that adding functionally identical (or substitutable) species to the community will have no effect on ecosystem functioning (Fig. 1). In theory, this is not entirely accurate because it ignores abundance effects. Functionally identical species will often have additive effects

at low densities but at increasing densities their combined effect will become increasingly sub-additive. This is because at high densities the functional role is more completely filled—in the case of predators and their prey, the prey population is eventually depleted (although total prey extinction is not certain and the proportion of prey that survives may be a function of the strength of predator interference). Thus, functionally identical species become functionally redundant at some critical abundance. This same logic applies to individuals of a single species: adding individuals to a population (e.g., predator population) will affect ecosystem functioning (e.g., herbivore suppression) until some critical abundance at which conspecifics become functionally redundant.

To improve the practice of CBC, we need to better understand how predator abundance, richness, and function are interrelated. Experiments that manipulate predator abundance and richness independently can make progress towards this goal. An experiment with the following treatments would be particularly valuable: 1) Low density, Low richness (typical of conventional agroecosystems), 2) High density, Low richness, and 3) High density, High richness (typical of organic agroecosystems). Such an experiment could be used to assess the independent effects of abundance and richness. Further, it could directly test the hypothesis that adding different predator species to an agroecosystem will lead to better biocontrol than adding more of the same predator species. This outcome would be expected if conspecifics become functionally redundant before heterospecifics, a prediction that makes sense because different species are more likely to be functionally diverse.

3.2. Species richness and composition

To evaluate the relationship between biodiversity and ecosystem functioning, plant studies have often examined how ecosystem functioning changes along a gradient of species richness (Loreau et al. 2002). At each level of species richness, communities with multiple species compositions are included. These species compositions are generated by random draws from a large species pool. In the statistical analysis, variance caused by species richness is assigned to the treatment term, while variance caused by species composition is assigned to the error term. Thus, this experimental approach attempts to isolate the effect of species richness by minimizing the influence of species composition (Huston and McBride 2002).

Few predator studies have attempted to distinguish between the effects of species richness and species composition (but see Finke and Denno 2005, Wilby et al. 2005). While predator ecologists may not have recognized this as an interesting or important distinction, there are probably additional reasons for this disparity between BEF and multiple-predator research. First, predator species richness is generally less than that of lower trophic-level consumers (Duffy 2003), a logistical constraint that limits the opportunity to experimentally address the problem. Predator ecologists often limit the available species pool even further by concentrating on strong interactors, or the subset of the predator community that most obviously affects prey population dynamics. Finally, predator ecologists have largely focused on the emergent effects of multiple predators on their prey. In these factorial experiments, the high richness treatment is composed of a single species composition. Thus, these studies all confound the effects of species richness with species composition.

A casual inspection of the multiple-predator literature reveals that species composition is extremely important. Examples of synergism (Soluk and Collins 1988, Losey and Denno 1998), antagonism (Rosenheim et al. 1993, Ferguson and Stiling 1996, Finke and Denno 2004, Snyder and Ives 2001), and additivity (Hurd and Eisenberg 1990, Snyder and Ives 2003) all exist, and this variation in predator-predator interactions is almost certainly caused by variation in species composition (although other factors may be important too). Obviously, these studies cannot be used to assess the value of species richness by themselves, because they each include only a single species composition. And while a meta-analysis of these studies would be a valuable exercise in its own right, it too would fall short of the goal of assessing the value of species richness. This is because, as we noted in the previous section, the additive designs most commonly employed by these studies confound the effects of species richness with density. Thus, experiments will have to be carefully designed to disentangle the effects of predator species richness and composition.

Recently, two well-designed predator studies have experimentally distinguished between the effects of predator species richness and composition (Finke and Denno 2005, Wilby et al. 2005). In each of these studies, multiple predator compositions were nested within each level of species richness, and the independent effects of species richness and composition were analysed. In both cases, the effect of species composition on herbivore suppression was significant. Further, Finke and Denno (2005) found an interaction such that increasing species richness led to weakened herbivore suppression in compositions that included intraguild predators, but not in compositions that excluded intraguild

predators. This study takes an important first step towards understanding why species compositions vary in their effectiveness.

While there is a growing need to assess whether predator species conservation and biological control are compatible goals, the primary objective of many CBC research programs will be to improve the biological control of pests. This will likely require the targeted conservation of specific species (Snyder et al. 2005). Thus, CBC researchers will want to know which species compositions are the most effective. Experiments that vary species composition to better isolate the effect of species richness also allow the researcher to screen for particularly effective compositions (e.g. Finke and Denno 2005, Wilby et al. 2005). In follow-up studies, particular species compositions may be selected to confirm, with greater replication, which combinations should be targeted for conservation. Unfortunately, there will often be a trade-off such that both species richness and composition cannot be powerfully tested in the same experiment: to test for the effect of species richness, many species compositions must be included; to test for the effect of species composition, species compositions should be replicated, which will often mean that fewer compositions can be included. As researchers in the field know all too well, BEF experiments reflect a complex mix of trade-offs, sacrifice and compromise (Allison 1999).

3.3. Species richness and identity

As we have noted, many BEF studies create communities with varying levels of richness by randomly drawing species (with replacement) from a large species pool. As a consequence of this experimental approach, the probability that any one species occurs in

a community increases with species richness. If a species with an extreme trait value that is important to the ecosystem function of interest occurs more often in richer communities, these communities may show higher (or lower, as the case may be) levels of functioning. Such sampling effects are caused by changes in species identity, not by changes in diversity per se (because species-poor communities may also include these key species). Further, they depend on the assumption that community assemblage is a random process, which is debatable (Hooper et al. 2005). Thus, whether sampling effects are an experimental artifact or a legitimate mechanism by which biodiversity affects ecosystem functioning has been debated (Loreau et al. 2001). This debate has important implications for biodiversity conservation because it can potentially affect whether resource managers focus their conservation efforts on one or few species, or on species richness more broadly.

Interestingly, a similar debate can be found in the classical biological control literature. On average, 3.4 natural enemy species have been released against each pest (Waage and Mills 1992). However, whether multiple species actually provide better control than a single species is uncertain (Myers 1985, Myers et al. 1989, Ehler 1990, Denno and Finke this volume, Janssen et al. this volume, Rosenheim and Harmon this volume). Myers (1985) proposed two models to explain how multiple introductions can lead to successful biological control. In the lottery model, multiple introductions increase the success of biological control by increasing the probability that a single, effective agent is introduced. In the cumulative stress model, multiple species act in an additive fashion and are cumulative in their suppressive effects on the target pest. The lottery and

cumulative stress models of classical biological control are directly analogous to the sampling and species complementarity effects of BEF research.

Denoth et al. (2002) analyzed the classical biological control record and found that in over 50% of multi-agent introductions against both weeds and arthropods, successful biological control was attributed to a single species. This result is consistent with the lottery model and supports the importance of species identity. Logistic regressions of biological control success (successful or not successful) on the number of agents released showed that increasing natural enemy species richness improved the biological control of weeds, but had no effect on arthropod pests. This result suggests that species complementarity (the cumulative stress model) may be more important for the classical biological control of weeds than it is for arthropods. To explain this, Denoth et al. (2002) hypothesized that weeds may be able to support multiple agents, e.g., foliage and seed feeders, while arthropods provide fewer opportunities for such resource partitioning. In other words, the link between taxonomic and functional diversity may be stronger for weed control agents than it is for arthropod control agents. This seems particularly likely given that multiple parasitoid species are often introduced for the biological control of arthropod pests. Unlike predators, parasitoids often attack and “kill” the same individuals (i.e., superparasitism, hyperparasitism). This is perhaps the clearest case of functional redundancy imaginable. Such functional redundancy may also explain why parasitoid species richness has no effect on total percent parasitism in grass-feeding chalcid wasps (Rodriguez and Hawkins 2000). Thus, the classical biological control record suggests that species identity, not richness, is the key to successful arthropod

biocontrol. Whether this conclusion can be extended to CBC, where the available species pool is not limited to a single functional group, remains an open question.

Numerous BEF studies have attempted to distinguish between sampling and species complementarity effects to assess whether the conservation of species richness itself is warranted. In plant studies where primary productivity is the response variable, measures of overyielding are commonly used to provide evidence for species complementarity. Numerous indices of overyielding have been developed, primarily as a tool to serve agriculture by maximizing plant yields through intercropping (Vandermeer 1989, Petchey 2003). Recently, BEF workers have developed more sophisticated statistical procedures for partitioning sampling and species complementarity effects (Loreau and Hector 2001, Špačková and Lepš. 2001, Petchey 2003). These procedures may be adapted by ecologists working with animals (Cardinale et al. 2002, Duffy et al. 2003). In addition to using statistical procedures to distinguish between sampling and species complementarity effects, researchers have also attempted to control experimentally for sampling effects to isolate the effects of species complementarity (e.g., Reich et al. 2004, Straub and Snyder 2006). By ensuring that the mean abundance of each species is equal across levels of species richness (as opposed to random or intentionally varied), differences between levels of richness cannot be caused by variation in the relative abundance of single species. This minimizes the potential for sampling effects. However, it is important to realize that controlling for species abundance is not the same as controlling for species occurrence. So while the mean abundance of any one species may be equal across levels of richness, it is still possible (and indeed likely) that a given species will be present in a greater proportion of high than low richness

communities. Thus, species identity is not entirely controlled and the potential for sampling effects has not been completely eliminated. Nevertheless, controlling for species abundance is an important advance in experimental methodology and can strengthen investigations into the effects of increasing predator species richness.

4. The importance of extraguild prey diversity

In most communities, predators have multiple prey types to choose from. Wilby and Thomas (2002a) have argued that the value of predator diversity will depend on the diversity of prey types that are present. Specifically, they used a simulation model to show that suppression of exopterygote pests will not be affected by increasing predator biodiversity because there is little opportunity for resource partitioning among predator species when there are few phenotypic differences among prey life stages. Multiple predator species are thus functionally redundant, and of neutral value, in the case of exopterygotes. In contrast, endopterygotes, which have phenotypically diverse life stages (i.e., egg, larvae, pupae, adult), provide ample opportunity for resource partitioning among predator species and are thus more effectively controlled by a diverse predator assemblage. Here predator species fill different functional roles by attacking different prey life stages and, through resource partitioning, multiple predators act additively to suppress their prey. Ives et al. (2005) used a mathematical model to demonstrate an analogous situation. In their model predator species varied in their attack efficiencies on different prey species. Increasing predator diversity strengthened suppression of the entire prey community, but was of no value to the suppression of single prey species where there was no opportunity for resource partitioning among predator species. The

hypothesis that the value of predator diversity depends on the diversity of the prey base has clear implications for biological control: increasing predator biodiversity will be important when the pests are endopterygotes and/or there are several target pest species. Surprisingly, few multiple-predator studies have included more than one prey species or life stage, leaving this simple hypothesis largely untested.

In addition to providing a substrate for resource partitioning and thus additivity among predator species, including multiple prey species can modify the interactions among predators and focal pests in important ways (e.g., Cardinale et al. 2003). For example, Cardinale et al. (2003) examined how *Coccinella* sp., *Nabis* sp., and the parasitoid *Aphidius ervi* combine to control the pea aphid in alfalfa. Adding these natural enemies together led to synergistic suppression of the pea aphid. Interestingly, this outcome depended on the presence of a second herbivore. In addition to pea aphids, the study also included cowpea aphids, which commonly occur in alfalfa but achieve pest status only rarely. Apparently, the presence of the cowpea aphid caused the parasitoid to attack the pea aphid less often. When all three natural enemies were present, *Coccinella* reduced cowpea aphid densities, thus causing the parasitoid to attack pea aphids more often. This interaction modification led to a positive emergent effect such that pea aphid suppression was greater in the high diversity treatment than would be expected based on the individual impacts of each natural enemy when alone.

The takehome message, then, is that the value of increasing predator biodiversity may often depend on the diversity of the available prey base. Most agroecosystems have multiple pest species as well as herbivores that do not achieve pest status. To accurately

evaluate the consequences of increasing predator biodiversity for biological control, these community members should be included in experiments whenever possible.

5. Conclusions

With predator biodiversity increasing in response to organic agriculture while global declines in biodiversity continue at an unprecedented rate, CBC researchers are now finding themselves at the intersection of biological control, sustainable agriculture, and biodiversity conservation. A deeper understanding of the relationship between predator biodiversity and biological control is needed to assess the compatibility of biodiversity and biocontrol and to improve the efficacy of CBC programs. BEF researchers have recognized that biodiversity is a complex concept that includes species richness, abundance, composition, and identity. While these components of biodiversity are often correlated, they may each be important to varying degrees. Thus, BEF researchers have developed an experimental framework that may be used to isolate their independent effects in an effort to identify which of these components should be prioritized for conservation. This approach can be easily extended to the higher trophic levels that CBC researchers work with. We see an important opportunity here, and provide several suggestions for how CBC researchers might proceed.

First, CBC researchers will want to extensively survey their agroecosystem, and perhaps the surrounding landscape, to identify the species pool from which they will work (see van Veen, this volume, for related discussion). Predator species that do not obviously impact target pests should not be ignored, because these species may still have important indirect effects (Wootton 1994). For the same reason, apparently unimportant

herbivores and detritivores should be included as well. We are well aware of the logistical demands of collecting so many species, and appreciate that no study can account for all of the biocomplexity in the system. Further, we recognize that by including so much complexity, the underlying mechanisms will not be easily revealed. However, we cannot ignore this complexity if we want to accurately assess the effect of increasing predator diversity on biological control. Thus, a top-down approach that embraces complexity and compares communities with natural or elevated levels of species richness to less speciose predator communities should be used to measure the effect of species richness on biological control. As we have discussed in this essay, BEF-type experiments can be used to identify the components of predator biodiversity that are responsible for the observed pattern. And once this pattern is generated, hypotheses about the species interactions that are at work can be formulated and, in the tradition of much predator ecology research, we can create much simpler communities to examine these interactions more closely.

An important incongruence between CBC and BEF research is that the latter has generally ignored the effects of abundance, yet this component of biodiversity is at least as relevant to CBC as is species richness. Thus, experiments that manipulate both predator abundance and richness will be extremely valuable. Further, we see the integration of abundance and richness effects as a priority for CBC research, and as an exciting opportunity to make an important contribution to our understanding of biodiversity and ecosystem functioning more generally.

Finally, consistent differences between organic and conventionally managed fields in predator species richness, abundance, composition or identity provide an

obvious platform for experimental work. Alternatively, researchers may want to use their agroecosystem as a model system to examine how increasing predator species richness affects biological control. Almost no experiments have properly isolated the effect of predator species richness on biological control, making this an important objective. And while logistically difficult, creating a gradient of predator species richness and measuring pest suppression and/or primary production (i.e., trophic cascades) would be particularly valuable. It is a reasonable hypothesis that, because predator species can both compete with and eat each other, they are fundamentally different from other consumers and will thus produce a very different diversity-function relationship than has been observed with plants (Fig. 1). Alternatively, as we have alluded to, interspecific interference may not be so severe and a similar diversity-function relationship may exist. Research on this problem is needed from the perspective of both CBC and BEF, and will help to evaluate the compatibility of biodiversity conservation and biological control.

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CHAPTER 2

SPECIES IDENTITY DOMINATES THE RELATIONSHIP BETWEEN PREDATOR BIODIVERSITY AND HERBIVORE SUPPRESSION

Abstract. Agricultural pest suppression is an important ecosystem service that may be threatened by the loss of predator diversity. This has stimulated interest in the relationship between predator biodiversity and biological control. Multiple-predator studies have shown that predators may complement or interfere with one another, but few experiments have determined if the resulting effects on prey are caused by changes in predator abundance, identity, species richness, or some combination of these factors. We experimentally isolated the effect of predator species richness on the biological control of an important agricultural pest, the green peach aphid. We found no evidence that increasing predator species richness affects aphid biological control; overall there was no strong complementarity or interference among predator species that altered the strength of aphid suppression. Instead, our experiments revealed strong effects of predator species identity, because predators varied dramatically in their per-capita consumption rates. Our results are consistent with other multiple-predator studies finding strong species identity effects and suggest that, for the biological control of aphids, conservation strategies that directly target key species will be more effective than those targeting predator biodiversity more broadly.

INTRODUCTION

Agricultural pest suppression has been identified as an important ecosystem service that may be threatened by the loss of predator biodiversity (Kruess and

Tscharntke 1994, Wilby and Thomas 2002), and it has been suggested that pest outbreaks are common in conventional agroecosystems because these simplified systems are species-poor (Pimentel 1961). These ideas suggest that managing for greater predator diversity will improve pest suppression, yet only a few experimental studies have explicitly examined the relationship between predator biodiversity and biological control (Cardinale et al. 2003, Finke and Denno 2004, Aquilino et al. 2005).

Numerous studies have investigated the relationship between biodiversity and ecosystem functioning (BEF) (Loreau et al. 2001, Hooper et al. 2005). While these studies have focused primarily on lower trophic levels in natural systems, the knowledge gained from this body of work may be usefully applied to predators in managed systems (Wilby and Thomas 2002, Ives et al. 2005). For example, from BEF studies it has become apparent that increasing the diversity of consumer communities almost invariably leads to greater total resource (= prey) consumption (Loreau et al. 2001). This biodiversity effect is driven by two distinct mechanisms, *species complementarity* and the *sampling effect* (Loreau et al. 2001). Species complementarity occurs through resource partitioning, when species utilize resources in different ways and combine to consume more than any single species would by itself; and through facilitation, when the presence of one species increases resource consumption by another species (Loreau et al. 2001). The sampling effect refers to the higher probability that species-rich communities will include dominant species with unusually high (or low) consumption rates. Like species complementarity, the sampling effect can increase community consumption, but this latter mechanism depends on the identity of one or a few species and not on greater diversity *per se*. BEF experiments have attempted to distinguish between these two

mechanisms to identify the components of biodiversity that must be conserved to prevent the deterioration of ecosystem functioning (Loreau and Hector 2001, Tilman et al. 2001, Cardinale et al. 2002). Likewise, distinguishing between species complementarity and sampling effects can provide guidance on whether conservation biological control practitioners should manage for greater species richness, a greater abundance of a few dominant species, or both components of predator biodiversity.

In terrestrial predator systems, there is experimental evidence for both species complementarity (Losey and Denno 1998, Cardinale et al. 2003, Aquilino et al. 2005) and species identity effects (Schmitz and Suttle 2001, Schmitz and Sokol-Hessner 2002). In addition, numerous studies have highlighted the importance of interference among predators (Rosenheim et al. 1993, Ferguson and Stiling 1996, Snyder and Ives 2001, Finke and Denno 2004). Thus, adding predators to a community may enhance (Losey and Denno 1998, Cardinale et al. 2003, Aquilino et al. 2005) or disrupt (Rosenheim et al. 1993, Snyder and Ives 2001, Finke and Denno 2004) herbivore suppression. However, few studies have been designed to determine whether multiple-predator impacts on prey are caused by changes in predator abundance, identity, richness, or some combination of these factors (but see Aquilino et al. 2005).

In the present study, we examined how increasing predator diversity affects the biological control of an important agricultural pest, the green peach aphid (*Myzus persicae*), on potato (*Solanum tuberosum*). Our experimental design allowed us to distinguish between the effects of predator species richness (species complementarity and interference) and species identity (sampling effects).

METHODS

The study was conducted at the Washington State University Othello Research Station in southcentral Washington. Our focal pest, the green peach aphid, is one of the most economically damaging herbivores of potatoes in Washington (Koss et al. 2005). Locally, a diverse community of predators attack green peach aphid in potatoes [the predator community has been detailed by Koss et al. (2005)]. Six of these taxa (called species for simplicity) were used in the work reported here (Table 1). We would have liked to examine all of the levels of species richness and species compositions that are possible with this species pool, but this was logistically impractical. Thus, we conducted two separate experiments with different richness levels and species compositions to broaden our search for diversity effects.

The predators in our system show considerable variation in their foraging behavior (Table 1). This trait diversity may lead to complementary resource-use. For example, the ladybird beetle *Coccinella septempunctata* has been shown to cause aphids to drop to the ground where they are more likely to be consumed by the ground beetle *Harpalus pensylvanicus* (Losey and Denno 1998). However, intraguild predation may also occur among these predators. *Nabis* and *Geocoris* will feed on one another depending on which predator is in the larger developmental stage (Raymond 2000), *Harpalus* may consume *Nabis* (Snyder and Wise 2001), and many insect predators feed on aphid parasitoids (Brodeur and Rosenheim 2001). Given that both positive and negative interactions are possible among these predator species, we had no *a priori* expectations regarding the value of predator diversity in this system.

Our experimental mesocosms were 2 x 2 x 2 m cages with 32 x 32 mesh Lumite screening and a zipper on one side to allow entry (BioQuip, Gardena, California, USA). Cages were placed in a mature potato field and were randomly assigned to treatment. The cage bottom edges were buried under ~20 cm soil to reduce arthropod movement in and out of the cages, and each cage was thinned to include 4 plants. Foliar arthropods were removed with a D-vac suction sampler (Rincon Vitova, Ventura, California, USA) and by hand-searching, and ground arthropods were removed by pitfall trapping. After arthropod removal, aphids were added to the cages. All cages received an equal number of aphids on the same day, and the aphids were allowed 1-3 days to establish before the predators were re-introduced. Mean initial aphid densities were ~20 per cage in Experiment 1 and ~60 per cage in Experiment 2. The predators were field-collected by D-vacuuming, pitfall traps, and by hand, and were used 1-3 days after collection. *Aphidius matricariae* was obtained from laboratory colonies. For both experiments, the total density of predators per cage was within the range found in production potato fields (Koss and Snyder 2005).

Predator communities were assembled according to three treatments: Control (no predators added), Low species richness (1 predator species added), and High species richness (3-4 predator species added). Multiple predator effects can be examined with additive experimental designs, which elevate the total abundance of predators to examine interspecific interactions, or with substitutive experimental designs, which hold the total abundance of predators constant across levels of species richness (Sih et al. 1998). We used a substitutive experimental design because this approach isolates the effect of increasing species richness from the effect of increasing total predator abundance. Further, while both predator species richness and abundance may be conserved by the

adoption of more sustainable agriculture practices (Hole et al. 2005, Bengtsson et al. 2005), in Washington potatoes we have found that such practices often lead to greater predator *and* pest abundance (Koss et al. 2005). Thus, by holding the predator:prey ratio constant across levels of richness, the substitutive design may better reflect the biology of our system.

To further isolate the effect of predator species richness, we designed our experiments to minimize the possibility that species identity effects (i.e. sampling effects) would be responsible for differences between the species richness treatments. As species richness increases, so too does the probability that any one species will occur. Thus, if species X has an extreme trait value, then differences between treatments that vary in species richness might be caused by the greater representation of species X in the high richness treatment. To minimize this possibility, the predator species were distributed so that each species was equally represented in the Low and High richness treatments (for predator abundance manipulations, see Appendix A). For example, in Experiment 1, *Nabis*, *Geocoris*, *Coccinella*, *Misumenops* and *Harpalus* comprised 21%, 21%, 16%, 21%, and 21% of the predators in both the Low and High richness treatments (Appendix A). Thus, differences between richness treatments could not be caused by differences in the relative abundance of any one species.

The species pool in Experiment 1 included five taxa (Table 1). In the Low richness treatment, each predator community consisted of a single species, and each species monoculture was replicated four times ($n = 20$). In the High richness treatment, each predator community consisted of 3 species. There are 10 unique combinations of 3 from a species pool of 5. We used all 10 combinations, each replicated once, to minimize

the possibility that any one species combination would be responsible for differences between the richness treatments. By minimizing such *species composition* effects, this experimental design feature further isolates the effect of species richness (Tilman et al. 2001, Reich et al. 2004). The experiment was run for ten days.

Four species were included in Experiment 2 (Table 1). As in the first experiment, each of the natural enemy species was replicated four times in monoculture to create the Low richness treatment (n = 16). We increased the diversity gradient in Experiment 2 by including all four species in the High richness treatment (n = 9). As a trade-off, we were unable to vary species composition. We also extended the experiment to 20 days to allow more time for richness effects to manifest themselves. However, by day 10 aphid populations had substantially increased and we added more predators because, under natural conditions, predators aggregate in areas of high prey abundance in potato fields (Koss et al. 2005). We acknowledge that this predator addition may have obscured any effects of intraguild predation that occurred early in the experiment, and thus should encourage a positive relationship between predator species richness and prey suppression.

Predators were re-collected from all cages at the end of both experiments by D-vacuuming, pitfall trapping, and hand-searching. From these data, the richness and total abundance of predators were calculated for each of the three treatments.

Data analyses

Two-sample *t*-tests, ANOVA, and repeated measures MANOVA were used to test for treatment effects in SYSTAT (v. 9). We used two planned comparisons, predator addition (Low richness + High richness) vs. Control, and Low richness vs. High richness, to compare the richness and abundance of predators in the three treatments at the end of

the experiments. These same planned comparisons were used to measure the effect of predator addition, and the effect of increasing predator species richness, on aphid densities. The predator abundance data were log-transformed to improve normality and homogeneity of variance, and the aphid data were \log_{10} transformed to reflect exponential population growth.

The per-capita impact of each predator community-type was calculated using the equation: $\ln(N_{\text{predators absent}}/N_{\text{predators present}})/P$, where N = final aphid density and P = initial predator density (Wootton 1997). The mean for the no-predator Controls was used for the $N_{\text{predators absent}}$ term. We used the initial, rather than final, predator density because some species are more easily recovered than others (for example, *Coccinella* are more easily recovered than *Geocoris* because the former are larger, more brightly colored, and slower).

RESULTS

Despite differences in the conditions of Experiments 1 and 2, the results were similar. Thus, we present the results of both experiments simultaneously rather than presenting each experiment in turn.

Predator communities were more species-rich in the predator addition treatments (Low + High richness) than in the no-predator Control (Exp 1: $t = 2.109$, d.f. = 38, $P < 0.05$; Exp 2: $t = 4.106$, d.f. = 32, $P < 0.001$). The High richness treatment remained more predator species-rich than the Low richness treatment (Exp 1: $t = 2.544$, d.f. = 28, $P < 0.05$; Exp 2: $t = 4.537$, d.f. = 23, $P < 0.001$). Predators were more abundant in the predator addition treatments than in the Control (Exp 1: $t = 7.596$, d.f. = 38, $P < 0.001$;

Exp 2: $t = 11.538$, d.f. = 32, $P < 0.001$), but there was no difference in total predator abundance between levels of richness (Exp 1: $t = 0.886$, d.f. = 28, $P > 0.10$; Exp 2: $t = 0.178$, d.f. = 23, $P > 0.05$). See Appendix B for figure.

Aphid populations increased through time (Exp 1: Wilks' Lambda = 0.592, $F_{2,37} = 12.730$, $P < 0.001$; Exp 2: Wilks' Lambda = 0.260, $F_{3,30} = 28.490$, $P < 0.001$, Fig. 1) and the addition of predators significantly suppressed aphid population growth relative to the Control (Low richness + High richness vs. Control; Exp 1: $F_{1,38} = 10.442$, $P < 0.01$; Exp 2: $F_{1,32} = 5.727$, $P < 0.05$; Fig. 1). In Experiment 1, the strength of aphid suppression increased through time, leading to a significant treatment by time interaction (Wilks' lambda = 0.828, $F_{2,37} = 3.833$, $P < 0.05$). Separate ANOVAs on each sample date showed that predators significantly suppressed aphids on days 5 and 10 in this first experiment ($P < 0.01$). The corresponding treatment by time interaction in Experiment 2 was not significant (Wilks' lambda = 0.860, $F_{3,30} = 1.623$, $P > 0.10$).

While predators did exert significant biological control, increasing the richness of the predator community had no effect on the strength of aphid suppression in either experiment (Exp 1: treatment x time Wilks' lambda = 0.846, $F_{2,27} = 2.454$, $P > 0.10$; richness $F_{1,28} = 1.542$, $P > 0.10$; Exp 2: treatment x time Wilks' lambda = 0.980, $F_{3,21} = 0.142$, $P > 0.10$; richness $F_{1,23} = 0.072$, $P > 0.10$; Fig. 1).

We calculated the per-capita impact of each community-type to compare the strength of aphid suppression among predator communities (Fig. 2). Using this approach, we once again found that species richness (i.e. Low vs. High richness treatments) had no effect on aphid suppression (Exp 1: $t = 0.472$, d.f. = 28, $P > 0.10$; Exp 2: $t = 0.655$, d.f. = 23, $P > 0.10$; Fig. 2). Comparing each species in monoculture ($n = 4$ for each species), we

found a strong effect of species identity on the strength of aphid suppression (Exp 1: $F_{4,15} = 10.635$, $P < 0.001$; Exp 2: $F_{3,12} = 25.891$, $P < 0.001$; Fig. 2). *Nabis* and *Coccinella* provided the greatest biological control in Experiment 1, and *Coccinella* provided the greatest control in Experiment 2 (Fig. 2).

The variation in species composition within the High richness treatment in Experiment 1 provided us with an additional opportunity to look for species identity effects. Each species occurred in six of the ten communities. If these six communities have significantly more or less aphids than occurs in the remaining four communities, this can be taken as indirect evidence that the presence of the shared species is responsible for the difference. Using this approach, we looked for species identity effects for each of the five species. There was a significant species identity effect for one species; communities with *Coccinella* had significantly fewer aphids than those without *Coccinella* ($t = 2.444$, d.f. = 8, $P < 0.05$; Fig. 3).

DISCUSSION

Despite differences in experimental conditions, in both experiments we found that varying predator species richness had no effect on the strength of aphid suppression. Given that complementary resource-use has been shown to occur in communities of plants (Tilman et al. 2001, Reich et al. 2004), herbivores (Duffy et al. 2003) and filter-feeders (Norberg 2000, Cardinale et al. 2002), it is perhaps surprising that there was no evidence for species complementarity in the present study. However, one feature of our, and many other multiple-predator studies (e.g. Rosenheim et al. 1993, Ferguson and Stiling 1996, Snyder and Ives 2001, Denno and Finke 2004), is that we included a single

herbivore species as the resource base. By contrast, the plants, herbivores, and filter-feeders almost certainly utilized various resource types in the studies mentioned above. Indeed, many of the studies showing a positive relationship between increasing predator species richness and the strength of herbivore suppression have included multiple prey species (Cardinale et al. 2003, Ives et al. 2005) or prey life stages (Wilby and Thomas 2002). This observation supports the idea that predator diversity may be less important for the biological control of single pest species with simple life histories (like aphids), where there is little opportunity for resource partitioning among predator species (Wilby and Thomas 2002).

While we found no evidence for species complementarity, it is also notable that there was little evidence for species interference. This result differs from those of numerous multiple-predator studies finding that interference increases with predator species richness (e.g. Rosenheim et al. 1993, Ferguson and Stiling 1996, Snyder and Ives 2001, Finke and Denno 2004). At least two explanations can account for the absence of a relationship between predator species richness and interference in our study. First, the experiments may not have been long enough to detect the positive indirect effects on prey that may result from predator interference (Snyder and Ives 2003). Second, intraguild predation may be of little importance to herbivore suppression in our system. For intraguild predation to significantly disrupt herbivore suppression, strong interactors must be the victims of intraguild predation (e.g. Rosenheim et al. 1993). Inspection of predator species abundances at the end of our experiments revealed no differences in abundance between richness treatments, with one exception: In Experiment 1, *Geocoris* was less abundant in the High than Low diversity treatment ($t = 2.546$, d.f. = 28, $P = 0.017$). So

while it is possible that *Geocoris* suffered intraguild predation in the High richness treatment, it appears that the strongest interactors in our system, *Coccinella* and *Nabis* (Fig. 2), did not.

This study adds to a growing list of studies finding that predator species identity is an important factor in prey suppression (Schmitz and Suttle 2001, Schmitz and Sokol-Hessner 2002, Chalcraft and Resetarits 2003, Denoth et al. 2002). While negative effects of species identity are possible, for example by including a strong intraguild predator that disrupts herbivore suppression, our study found only a positive effect of species identity with increasing species richness: communities that included *Coccinella* provided stronger herbivore suppression than communities without *Coccinella* (Fig. 3). Because predator interference did not increase with species richness, and because we found a positive effect of species identity in species-rich communities, it seems likely that greater predator species richness will improve aphid biological control through the sampling effect in our system. This is good news given that sustainable agricultural practices such as organic farming generally promote greater predator species richness (Hole et al. 2005, Bengtsson et al. 2005).

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

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Table 1. Taxa used in the experiments

Taxa	Experiment	Description	Notes
<i>Nabis americanoferus</i> , <i>N. alternatus</i> (Damsel bug)	1 & 2	Generalist, roaming, sit-and-wait, in foliage	Species indistinguishable with live specimens; both were used
<i>Geocoris bullatus</i> , <i>G. pallens</i> (Big-eyed bug)	1 & 2	Generalist, roaming, in foliage and on ground	Species indistinguishable with live specimens; both were used
<i>Misumenops lepidus</i> (Crab spider)	1	Generalist, sit-and- wait, in foliage	
<i>Harpalus</i> <i>pennsylvanicus</i> (Ground beetle)	1	Generalist, roaming, on ground and in low foliage	
<i>Coccinella</i> <i>septempunctata</i> , <i>C.</i> <i>transversoguttata</i> (Ladybird beetle)	1 & 2	Aphid specialist, roaming, in foliage	An equal mix of the two species was used
<i>Aphidius</i> <i>matricariae</i> (Aphid parasitoid)	2	Aphid specialist, roaming, in foliage	

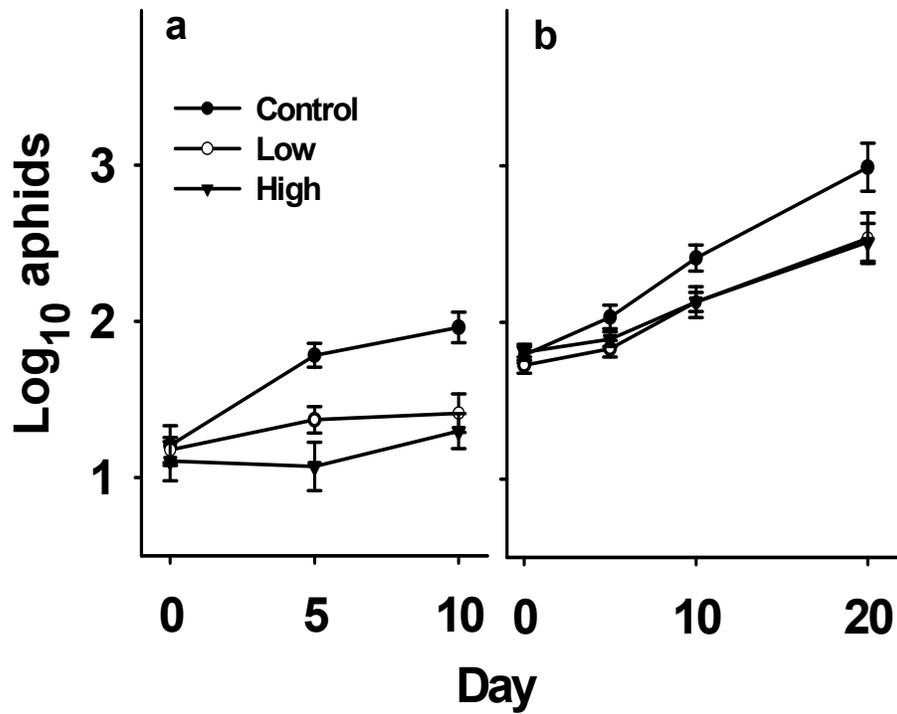


FIG. 1. Aphid densities through time in a) Experiment 1, and b) Experiment 2. Means \pm s.e.m. Aphid populations increased through time and the addition of predators suppressed aphid population growth relative to the no-predator Control. However, there was no effect of increasing the species richness of the predator community in either experiment.

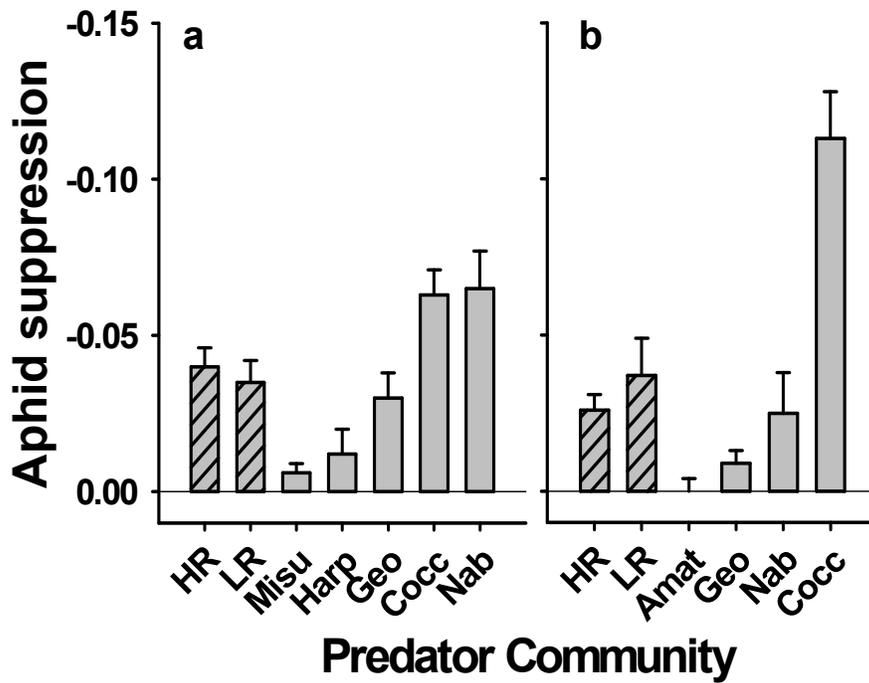


FIG. 2. Per-capita community impacts on aphid populations in a) Experiment 1, and b) Experiment 2. Values less than 0 indicate aphid suppression relative to the no-predator Control. HR = High richness, LR = Low richness, Misu = *Misumenops*, Harp = *Harpalus*, Geo = *Geocoris*, Nab = *Nabis*, Cocc = *Coccinella*, A mat = *Aphidius matricariae*. Means \pm s.e.m. Species richness did not affect aphid suppression (hatched bars), but species identity had a significant effect on aphid suppression (solid bars).

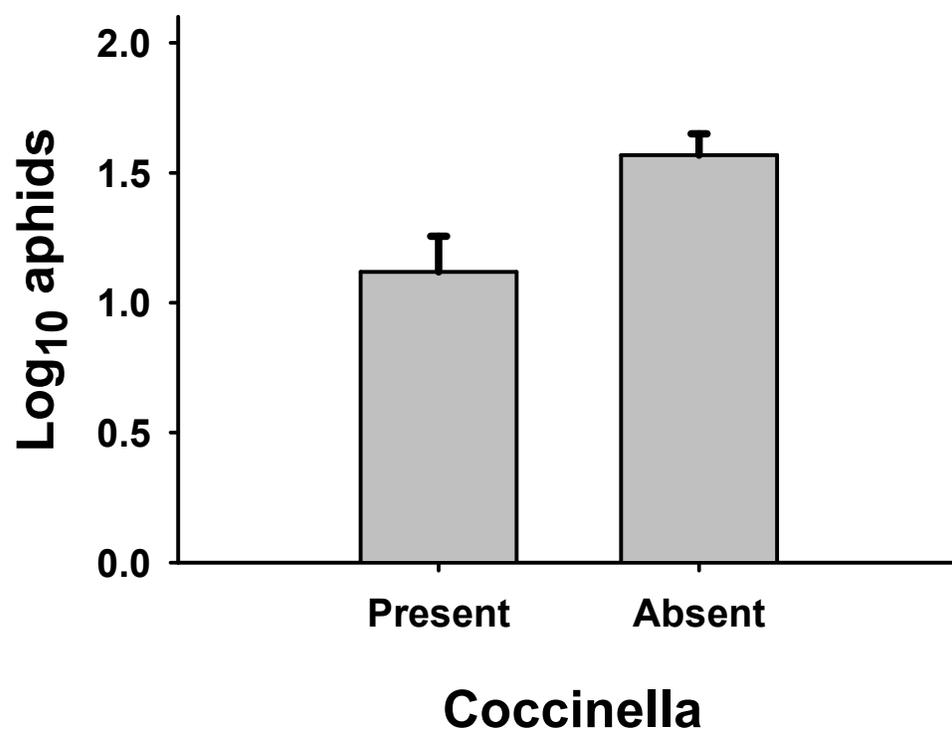


FIG. 3. Comparison of species-rich communities from Experiment 1. Means \pm s.e.m. Communities that included *Coccinella* (n = 6) provided significantly stronger aphid suppression than communities that excluded *Coccinella* (n = 4).

APPENDIX A

Table A1. Predator abundance manipulations in Experiments 1 and 2.

Exp	Richness treatment	Predator	Number of replicates in which the predator occurred	Predator abundance in these replicates	Predator abundance across replicates	Percentage of total predator abundance	
1	Low (1 taxon)	<i>Nabis</i>	4	48	192	~21	
		<i>Geocoris</i>	4	48	192	~21	
		<i>Coccinella</i>	4	36	144	~16	
		<i>Misumenops</i>	4	48	192	~21	
		<i>Harpalus</i>	4	48	192	~21	
	Total =					912	100
	High (3 taxa)	<i>Nabis</i>	6	16	96	~21	
		<i>Geocoris</i>	6	16	96	~21	
		<i>Coccinella</i>	6	12	72	~16	
		<i>Misumenops</i>	6	16	96	~21	
		<i>Harpalus</i>	6	16	96	~21	
	Total =					456	100
	2	Low (1 taxon)	<i>Nabis</i>	4	64	256	~23
			<i>Geocoris</i>	4	84	336	~31
<i>Coccinella</i>			4	28	112	~10	
<i>Aphidius</i>			4	100	400	~36	
Total =					1104	100	
High (4 taxa)		<i>Nabis</i>	9	16	144	~23	
		<i>Geocoris</i>	9	21	189	~31	
		<i>Coccinella</i>	9	7	63	~10	
		<i>Aphidius</i>	9	25	225	~36	
Total =					621	100	

Notes: The table shows how the predator taxa were distributed so that each taxon is equally abundant in the Low and High richness treatments. In Experiment 2, the

abundances reflect the total of both predator releases. The sex ratio for *Aphidius* was ~1:1.

APPENDIX B

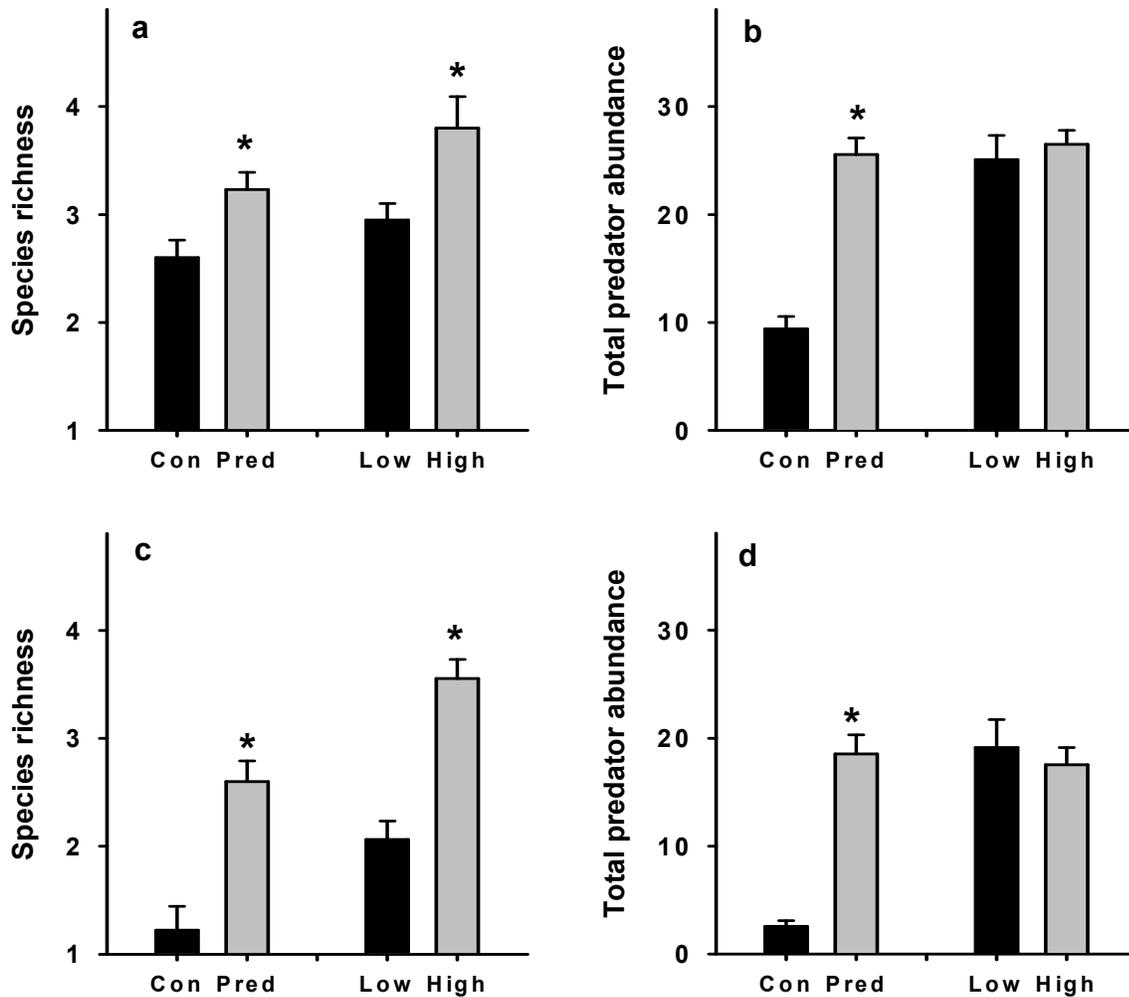


FIG. B1. Predator species richness and abundance at the end of Experiment 1 (a, b) and Experiment 2 (c, d). Con = no-predator Control, Pred = Predator addition treatments (Low + High richness), Low = Low richness, High = High richness. Means \pm s.e.m. Asterisks (*) indicate a significant difference ($P < 0.05$). Predator communities were more species-rich in the predator addition treatments than in the Control, and were more species-rich in the High than Low richness treatments. Predators were also more abundant in the predator addition treatments than in the Control, but there was no difference in predator abundance between richness treatments in either experiment.

CHAPTER 3

POSITIVE, NEGATIVE, AND NEUTRAL EFFECTS OF PREDATOR DIVERSITY ON HERBIVORE SUPPRESSION DRIVEN BY VARIATION IN SPECIES COMPOSITION

Abstract. Studies in different systems have reported positive, negative or neutral relationships between predator biodiversity and herbivore suppression, suggesting system-specific roles for predator diversity. We manipulated the species richness and species composition of predators attacking two herbivores of potato, the green peach aphid (*Myzus persicae*) and the Colorado potato beetle (*Leptinotarsa decemlineata*), and measured the impact of these manipulations on herbivore suppression. Our design included multiple replicates of each predator species in monoculture and multiple replicates of five multi-species predator communities varying in species composition, so that we could determine the relationship between predator diversity and herbivore suppression across all compositions, and within each sub-group of predator species. Overall, there was a net negative effect of increasing predator diversity on aphid suppression, with most predator compositions trending toward weakened prey exploitation with increasing predator diversity. In contrast, there was no consistent effect of predator diversity on potato beetle control, with different predator compositions exhibiting stronger, weaker, or unaltered suppression with increasing predator diversity. Thus, within a single system we found all of the relationships between predator diversity and herbivore suppression that have been reported in other studies, highlighting the

strong role for predator composition effects in mediating the relationship between predator biodiversity and herbivore suppression.

INTRODUCTION

Ecologists have grown increasingly concerned that species loss, which is occurring at an unprecedented rate (Thomas et al. 2004), will impair ecosystem functioning and lead to declines in the goods and services provided by ecosystems (Hooper et al. 2005). Experimental studies have shown declines in the efficiency of resource capture as species are lost from communities of plants (Hector et al. 1999, Tilman et al. 1997), herbivores (Naeem and Li 1998, Duffy et al. 2003), and filter-feeders (Norberg 2000, Cardinale et al. 2002). Such studies validate the concern that species loss may disrupt important ecological processes and provide a compelling reason to conserve biodiversity.

Unlike lower trophic levels where increasing diversity consistently leads to more efficient resource use (Tilman et al. 1997, Naeem and Li 1998, Hector et al. 1999, Norberg 2000, Cardinale et al. 2002, Duffy et al. 2003), there appears to be no consistent relationship between predator diversity and the key ecosystem function that predators provide, the suppression of herbivore populations. Various studies in different communities have found that increasing predator diversity can strengthen (Cardinale et al. 2003, Aquilino et al. 2005, Wilby et al. 2005), weaken (Rosenheim et al. 1993, Snyder and Ives 2001, Finke and Denno 2004, 2005), or not affect the top-down suppression of herbivore populations (Rodriguez and Hawkins 2000, Schmitz and Sokol-Hessner 2002,

Straub and Snyder 2006a). Thus, at present, the predator-prey literature suggests an idiosyncratic relationship between predator biodiversity and herbivore suppression.

It is unclear whether the apparent idiosyncrasy of predator diversity effects across systems reflects different relationships between predator diversity and herbivore suppression in different communities, or instead simply reflects the particular array of predator species considered. Often, studies include only a single diverse predator species composition (e.g., Sih et al. 1998 and references therein, Snyder and Ives 2001, Cardinale et al. 2003, Finke and Denno 2004, Aquilino et al. 2005, Byrnes et al. 2005; but see Bruno et al. 2005, Finke and Denno 2005, Wilby and Thomas 2005, Straub and Snyder 2006a), which makes it difficult to separate predator composition effects from those of predator species diversity *per se* (Wilby et al. 2005). Integrating the approaches typical of multi-species predator-prey interaction studies with those typical of biodiversity and ecosystem functioning studies looks to be a fruitful endeavor (Ives et al. 2005, Tscharrntke et al. 2005), but will require that both components of predator biodiversity, species richness and species composition, be experimentally manipulated to assess their independent effects.

Here, we investigate the relationship between predator biodiversity and the suppression of two herbivores, the green peach aphid (*Myzus persicae*) and the Colorado potato beetle (*Leptinotarsa decemlineata*), attacking potato (*Solanum tuberosum*). We manipulated both predator species richness and composition in a large-scale field experiment to address three questions: 1) What is the overall effect of increasing predator diversity on herbivore suppression? 2) Does predator species composition affect the strength of herbivore suppression? 3) Does the effect of increasing predator diversity vary

among species compositions, as might be expected from the range of predator diversity effects that have been observed across studies using different combinations of predator species?

METHODS

The study was conducted at the Washington State University Othello Research Station in south central Washington State. In Washington potato fields a diverse community of predators attacks the two numerically dominant herbivores, the green peach aphid, *M. persicae*, and Colorado potato beetle, *L. decemlineata* (Koss et al. 2005). Of the predator species, in our experiment we included the big-eyed bug *Geocoris pallens*, the damsel bug *Nabis spp.*, the ladybird beetle *Hippodamia convergens*, the green lacewing *Chrysoperla spp.*, and the predatory stinkbug *Podisus maculiventris*. These species were selected because each is known to feed on both aphids and potato beetles, to varying degrees, on potatoes (Biever and Chauvin 1991, Nordlund et al. 1991, Snyder and Clevenger 2004, Koss et al. 2005, Koss and Snyder 2005, Appendix A). All of the predators were released as adults, because colonization of annual cropping systems like potatoes is generally by winged adults (Wissinger 1997). The one exception was the green lacewing, which was released as 2nd instar larvae because it is only the immature stage that is predaceous (Canard et al. 1984). *Geocoris*, *Nabis*, and *Hippodamia* were field collected with a D-vac suction sampler (Rincon-Vitova, Ventura, CA, USA) or by hand. *Chrysoperla* and *Podisus* were obtained from a commercial insectary (Rincon-Vitova, Ventura, CA, USA).

Our experimental mesocosms were 2 x 2 x 2 m cages with 32 x 32 mesh Lumite screening and a zipper on one side to allow entry (BioQuip, Gardena, California, USA).

Cages were placed in two rows and the cage bottom edges were buried under ~20 cm soil to block arthropod movement in and out of the cages. Five, 20-day-old potted potato plants were placed in each cage and dug into the soil so that the lip of the pot was ~1 cm above the soil surface. The potato plants were grown in a greenhouse (16:8 L:D, 23 °C) and were free of herbivores before the experiment was initiated. Each cage then received 280 aphids and 14 potato beetle egg clutches containing 20 eggs each (total number of potato beetle eggs/cage = 280). Predators were introduced four days later, at a density of 36 predators/cage, which is within the range of predator densities found in Washington potato fields (Koss and Snyder 2005).

Eleven experimental predator communities (called treatments) were created, including five Low species richness treatments, five High species richness treatments, and one no-predator Control treatment. Low cages received 36 individuals of a single predator species, while High cages received 12 individuals of each of three different predator species. This substitutive experimental design isolates the effect of increasing species richness by maintaining constant total predator abundance across treatments (Sih et al. 1998). For Low, each of the five predator species in monoculture was replicated four times ($n = 20$ replicates). For High, we chose five of the ten possible three-species compositions with the requirement that each predator species appear the same number of times: *Podisus*, *Nabis*, *Chrysoperla* (PNC); *Podisus*, *Nabis*, *Hippodamia* (PNH); *Podisus*, *Hippodamia*, *Geocoris* (PHG); *Geocoris*, *Nabis*, *Chrysoperla* (GNC); and *Chrysoperla*, *Hippodamia*, *Geocoris* (CHG). Note that differences between the species richness treatments could not be caused by differences in the initial abundance of any one predator species because the mean abundance of each species was equal in the Low and High

richness treatments (Straub and Snyder 2006a). Each of the three-species compositions was replicated four times for a total of 20 High richness replicates.

The experiment was terminated at 21 days, at which time all aphids were counted, and all remaining potato beetles were collected. Potato beetles were both counted and weighed in the laboratory. Whether potato beetle abundance or weight was used in the analyses had no effect on the final results, and so only the number of remaining potato beetles is presented here. Predators were collected at the end of the experiment by D-vacuuming each cage for ~1 minute, followed by a visual inspection of each plant for ~30 seconds, and then by pitfall trapping (four traps were opened for 48 hours).

Data analyses

The herbivore and predator abundance data failed to meet ANOVA's assumption of normality, and so were rank transformed. ANOVAs (PROC GLM), followed by planned contrasts (CONTRAST), were conducted on these rank-transformed data in SAS version 8.2 (SAS Institute, Inc., 2003). Separate analyses were conducted on aphids and potato beetles (all significant differences detected with these univariate tests were also significant when we used multivariate tests, but for clarity only univariate tests are presented). One-way ANOVAs were used to determine if any differences existed among the eleven experimental treatments. This global analysis was followed by a series of planned contrasts. The first contrast examined the effect of predator addition by comparing the no-predator Control (n = 6 replicates) to the average of the treatments that contained predators (n = 40 replicates). The second contrast examined the effect of overall predator diversity by comparing the average of all Low richness treatments to the average of all High richness treatments. The third contrast examined the effect of

predator species composition by comparing the five different compositions of three species, i.e., the High richness treatments. Finally, by comparing each of the five three-species compositions (i.e., each High richness treatment) to the average of their three respective constituent species in monoculture, we tested the hypothesis that diversity effects varied with predator species composition. If a three-species composition performed significantly better or worse than the average of its three constituent species in monoculture, this was taken as evidence for a positive or negative effect, respectively, of increasing predator diversity. Because this series of contrasts involved ten separate comparisons (5 predator compositions x 2 herbivore response variables), potentially inflating the risk of committing a Type 1 error, we adjusted our critical *P*-value using the sequential Bonferroni correction (Rice 1989).

Final predator densities were examined to determine if positive and negative effects of predator diversity on prey suppression were related to differences between the Low and High richness treatments in final predator abundance. One-way ANOVA was used to determine whether final predator abundances differed among the eleven experimental treatments. This global analysis was followed by planned contrasts to determine whether total predator abundance differed between the Low and High richness treatments for all compositions combined, and then for each of the five species compositions alone. This analysis was conducted for adults, juveniles produced in situ, and for adults and juveniles combined.

RESULTS

The global analysis revealed significant variation among the experimental treatments for both aphid ($F_{10, 35} = 19.29, P < 0.0001$) and potato beetle abundance ($F_{10,$

$_{35} = 17.06, P < 0.0001$). The addition of predators (comparison of no-predator Control to the average of all treatments with predators) significantly reduced the abundance of both aphids ($F_{1,44} = 48.63, P < 0.0001$) and potato beetles ($F_{1,44} = 68.99, P < 0.0001$).

Overall, there was a negative effect of increasing predator diversity on the suppression of aphids ($F_{1,38} = 8.05, P = 0.0075$) (Fig. 1, top row). In contrast, increasing predator diversity had no overall effect on potato beetle suppression ($F_{1,38} = 0.62, P = 0.4361$) (Fig. 1, middle row).

There was significant variation among the five three-species predator compositions in the final abundance of both aphids ($F_{4,15} = 5.60, P = 0.0014$) and potato beetles ($F_{4,15} = 4.59, P = 0.0044$) (Fig. 2). The effect of increasing predator diversity also varied with species composition (Fig. 1, Appendix B). For the green peach aphid, most High richness predator compositions trended towards weaker aphid suppression than would be predicted, in the absence of emergent diversity effects, from the performance of the three constituent species in monoculture (Fig. 1, top row of panels). The pattern was more complex for Colorado potato beetle suppression (Fig. 1, middle row of panels). For this prey species, herbivore suppression increased with predator diversity within one composition (PHG), was disrupted within a second composition (PNH), and was unchanged within the remaining three compositions (PNC, CHG and GNC).

Final predator abundance differed among the experimental treatments for adults ($F_{10,35} = 3.38, P = 0.0036$), juveniles ($F_{10,35} = 3.84, P = 0.0014$), and for both stages combined ($F_{10,35} = 3.92, P = 0.0012$). However, when the average of all Low richness treatments was compared to the average of all High richness treatments, there was no

effect of diversity on final predator abundance for adults ($F_{1,38} = 0.24, P = 0.6308$), juveniles ($F_{1,38} = 0.01, P = 0.9376$), or both stages combined ($F_{1,38} = 0.30, P = 0.5850$). Similarly, there was no effect of increasing diversity on final predator abundance within any of the five species compositions (Fig. 1, bottom row; Appendix C).

DISCUSSION

Averaged across all compositions, increasing predator diversity led to weakened aphid suppression but had no net impact on potato beetle suppression (Fig. 1). Inspection of predator diversity effects within the different species compositions revealed considerable variation, with greater predator diversity sometimes strengthening, sometimes weakening, and sometimes not affecting the strength of herbivore suppression among these subsets of the predator species pool (Fig. 1, Appendix B). Notably, the effect of increasing predator diversity within these compositions also differed for the two herbivore species. Thus, the results of this study suggest that the effect of predator diversity may depend on both predator species composition and on herbivore species identity.

There was significant variation among the five three-species predator compositions in the strength of both aphid and potato beetle suppression. These composition effects were also influenced by herbivore identity: One predator composition was relatively effective against only aphids (CHG), two compositions were relatively effective against only potato beetles (PNC, PHG), one composition effectively suppressed both herbivores (GNC), and one composition was relatively ineffective against both herbivores species even though the constituent species were effective in

monoculture (PNC) (Fig. 2, Appendix A). This result is consistent with other studies finding that changes in species composition can affect ecosystem processes in complicated ways, often explaining more of the variation in ecosystem functioning than do changes in diversity itself (e.g., Tilman et al. 1997, Downing 2005).

Our experimental design allowed us to include both more predator species in total, and more combinations of these species, than are usually included in experimental predator-prey studies (Sih et al. 1998, Ives et al. 2005). Nonetheless, a clear weakness of this experimental approach is that we gained relatively little insight into the mechanistic underpinnings of our results, a criticism of biodiversity-ecosystem functioning research generally (Huston 1997). Consistently weakened herbivore control by the predator composition including *Podisus*, *Nabis* and *Hippodamia* suggests predator-predator interference (Fig.1, Appendix B). While increasing predator diversity can lead to higher rates of intraguild predation and weakened herbivore suppression (Finke and Denno 2004, 2005, Ives et al. 2005), we detected no differences between the Low and High richness treatments in predator survivorship for this, and indeed all other, predator compositions (Fig. 1, bottom row; Appendix C). This suggests that some kind of non-lethal predator interference, which is a well-documented phenomenon (Moran and Hurd 1994, Mallampalli et al. 2002, Schmitz et al. 2004, Byrnes et al. 2005), may have contributed to our results here. Similarly, predator-predator interactions that improve herbivore suppression are known from other systems (Sih et al. 1998), but further work would be needed to explain the improved control of potato beetles we observed for the predator community including *Podisus*, *Hippodamia* and *Geocoris*. Thus, while experiments of the type reported here do not readily reveal mechanisms, they are useful

in identifying emergent biodiversity effects that warrant further, more mechanistic, study (Straub and Snyder 2006b).

Various studies, across a wide range of terrestrial systems, have reported that increasing predator diversity can enhance, not affect, or diminish the strength of herbivore suppression (e.g., Rosenheim et al. 1993, Rodriguez and Hawkins 2000, Snyder and Ives 2001, Schmitz and Sokol-Hessner 2002, Cardinale et al. 2003, Finke and Denno 2004, Aquilino et al. 2005, Straub and Snyder 2006a). These disparate results may be caused by variation across studies in system properties [e.g., prey diversity (Duffy 2002), prey identity (Wilby and Thomas 2002, Wilby et al. 2005), plant characteristics (White and Eigenbrode 2000, Snyder and Ives 2001), and habitat complexity (Finke and Denno 2002)] and/or by variation across studies in experimental approaches [e.g., experimental design (Straub and Snyder 2006b), experimental venue (Skelly 2002), and the spatial (Van de Koppel et al. 2005) or temporal (Bell et al. 2003) scale of the experiments]. However, our results demonstrate that within-system species composition effects can generate the full range of predator diversity-herbivore suppression relationships that have been observed. For example, had we chosen only a single species composition, we could have found positive, negative, or neutral effects of predator diversity on potato beetle suppression (Fig. 1, middle row of panels). While this is the first study to find concurrent positive, negative and neutral effects of predator diversity on herbivore suppression in the field, two recent laboratory studies have produced similar results: Finke and Denno (2005) increased the diversity of different predator species compositions and found negative and neutral effects on the abundance of a planthopper, *Proklesia dolus*, in cordgrass, and Wilby et al. (2005) found neutral and positive effects

of increasing predator diversity on the abundance of a planthopper, *Nilaparvata lugens*, and a moth, *Marasmia patnalis*, in rice. Together, these three studies show that species composition effects, even within a single system, can strongly affect the relationship between predator biodiversity and herbivore suppression. Fortunately, studies can average across multiple species compositions to produce more robust predictions about the ecological consequences of changing predator biodiversity. And because this approach minimizes the influence of within-system species composition effects, it may also facilitate the identification of other ecological factors that vary across systems and modify the relationship between predator biodiversity and herbivore suppression.

The apparent importance of species composition for predator systems raises an interesting question: Are compositional effects more important for predator-prey systems than for other consumer-resource systems? We suggest the answer may be yes, for two reasons. First, predators and prey often exhibit complex behavioral responses to one another [e.g., trait-mediated indirect effects (Schmitz et al. 2004)] that can make species composition effects particularly dramatic (Prasad and Snyder 2006). Second, higher trophic levels are often characterized by lower levels of species richness (Duffy 2002). At low levels of species richness, little functional redundancy among species is expected and, as a consequence, compositional effects should be relatively large. Having said this, the three- and four-predator-species assemblages that have been examined thus far almost certainly underestimate true levels of predator species richness, and to date studies of terrestrial predator-prey systems have considered only two levels of predator diversity (predators in monoculture versus diverse communities at one arbitrary level of species richness). Future studies spanning both multiple species compositions, and multiple

levels of species richness, will be needed to better assess the relationship between predator biodiversity and herbivore suppression.

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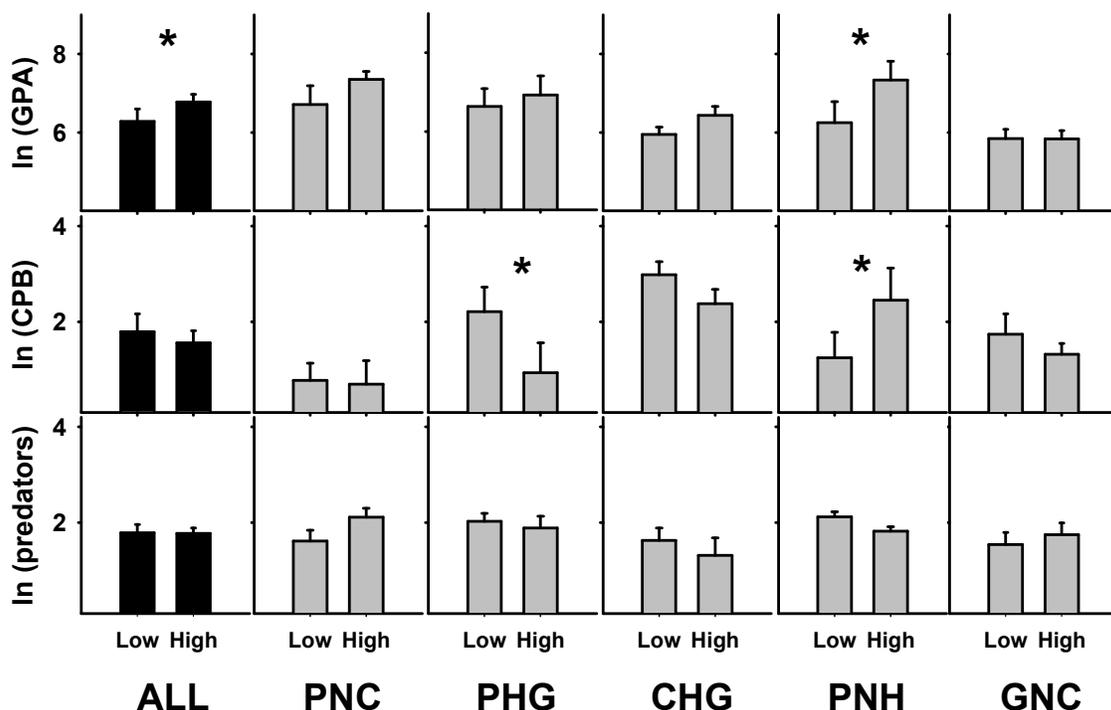


FIG. 1. Effect of increasing predator diversity on the suppression of green peach aphids, Colorado potato beetles, and on final predator abundance. The black bars (ALL) show the average of all the single species treatments (Low) compared with the average of all the three-species treatments (High) and thus provide a best estimate of the effect of predator diversity per se. The gray bars show the comparison of each three-species composition (High) to the average of its three respective constituent species in monoculture (Low). Note that the effect of predator diversity varied with predator species composition such that increasing diversity strengthened (PHG), weakened (PNH), and did not affect the strength of Colorado potato beetle suppression (PNC, GNC, CHG). GPA = green peach aphid, *Myzus persicae*; CPB = Colorado potato beetle, *Leptinotarsa decemlineata*; PNC = *Podisus*, *Nabis*, *Chrysoperla*; PHG = *Podisus*, *Hippodamia*, *Geocoris*; CHG = *Chrysoperla*, *Hippodamia*, *Geocoris*; PNH = *Podisus*, *Nabis*, *Hippodamia*; GNC = *Geocoris*, *Nabis*, *Chrysoperla*. Data are means \pm SE.

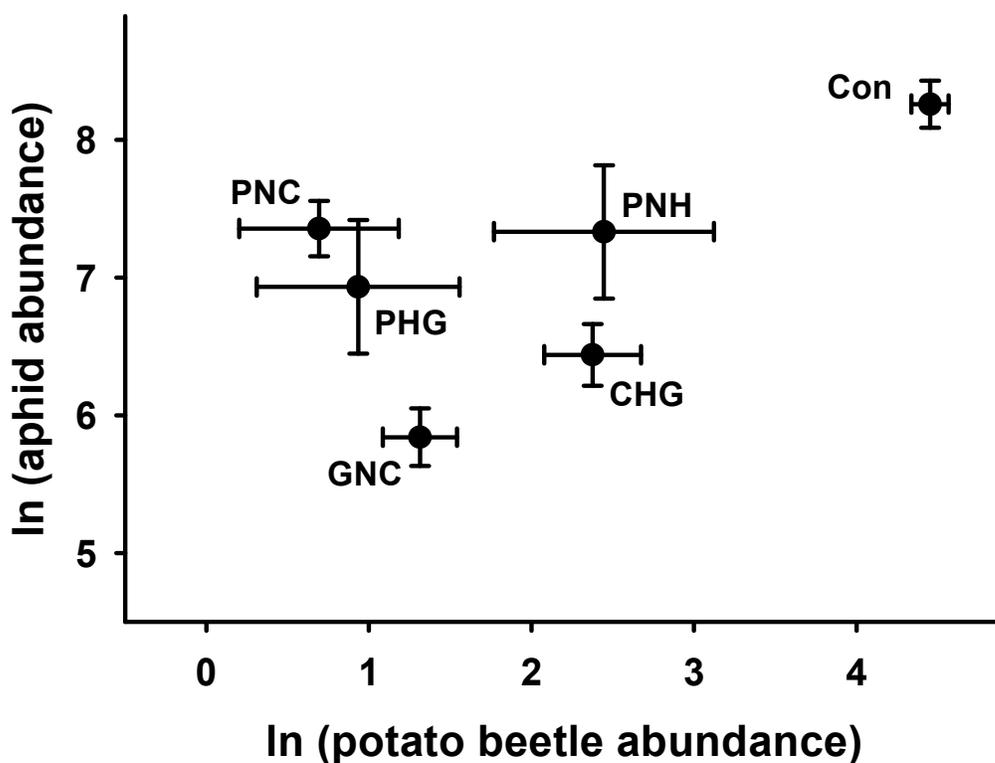


FIG. 2. Final abundance of green peach aphids and Colorado potato beetles in communities with different predator compositions. There was significant variation among species compositions for both aphid and potato beetle suppression. PNC = *Podisus*, *Nabis*, *Chrysoperla*; PHG = *Podisus*, *Hippodamia*, *Geocoris*; CHG = *Chrysoperla*, *Hippodamia*, *Geocoris*; PNH = *Podisus*, *Nabis*, *Hippodamia*; GNC = *Geocoris*, *Nabis*, *Chrysoperla*. Con = no-predator Control. Data are means \pm SE.

APPENDIX A

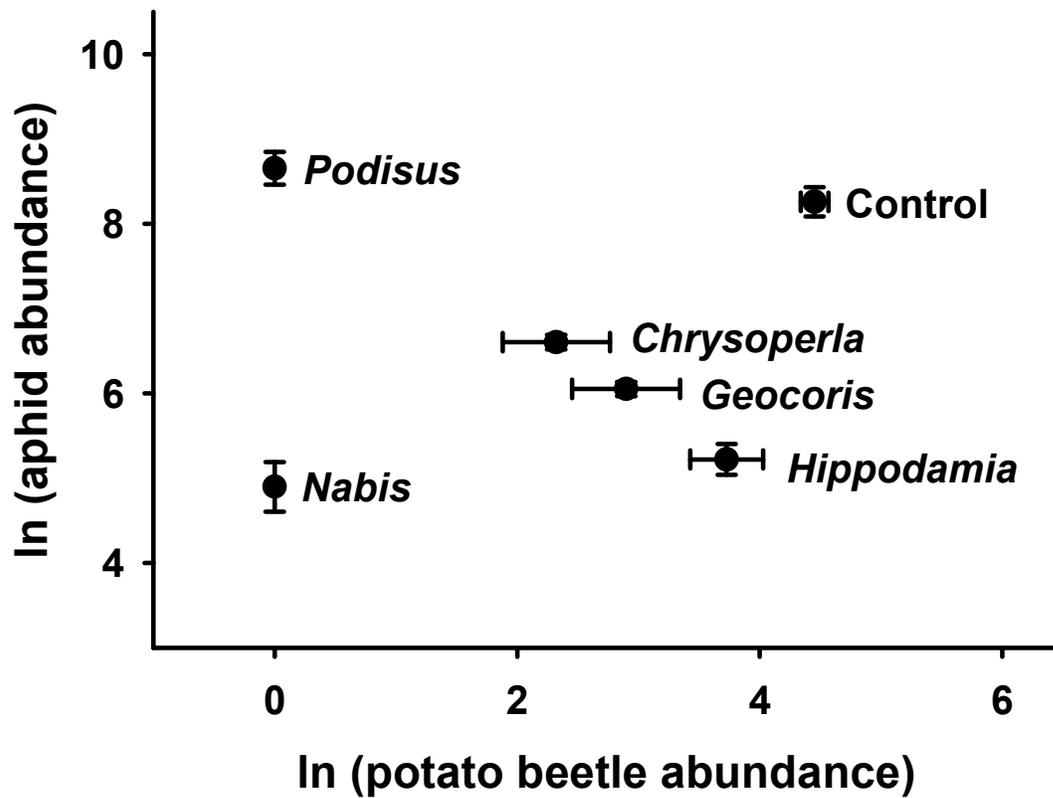


FIG. A1. The final abundance of aphids and potato beetles in treatments of each predator species in monoculture, and in the no-predator Control treatment. Data are means \pm SE.

APPENDIX B

Table B1. Table showing analyses of the effect of increasing predator diversity on the final abundance of aphids and potato beetles for five different species compositions.

Species Composition	Aphids			Potato beetles		
	DF	<i>F</i>	<i>P</i>	DF	<i>F</i>	<i>P</i>
Podisus, Nabis, Chrysoperla	1, 14	3.94	0.0551	1, 14	0.00	1.000
Podisus, Nabis, Hippodamia	1, 14	10.99	0.0021*	1, 14	8.75	0.0055*
Podisus, Hippodamia, Geocoris	1, 14	1.41	0.2437	1, 14	8.48	0.0062*
Geocoris, Nabis, Chrysoperla	1, 14	0.19	0.6657	1, 14	2.00	0.1659
Chrysoperla, Hippodamia, Geocoris	1, 14	2.95	0.0946	1, 14	0.62	0.4361

Notes: Significant differences between Low and High richness treatments are indicated by asterisks.

APPENDIX C

Table C1. Table showing analyses of the effect of increasing predator diversity on the final abundance of predators for five different species compositions.

Species Composition	Adults			Juveniles			Adults + Juveniles		
	DF	<i>F</i>	<i>P</i>	DF	<i>F</i>	<i>P</i>	DF	<i>F</i>	<i>P</i>
Podisus, Nabis, Chrysoperla	1, 14	0.10	0.7495	1, 14	2.26	0.1416	1, 14	2.74	0.1066
Podisus, Nabis, Hippodamia	1, 14	1.15	0.2906	1, 14	0.00	0.9886	1, 14	2.05	0.1608
Podisus, Hippodamia, Geocoris	1, 14	0.15	0.7046	1, 14	0.08	0.7752	1, 14	0.69	0.4112
Geocoris, Nabis, Chrysoperla	1, 14	0.01	0.9099	1, 14	0.21	0.6480	1, 14	0.06	0.8028
Chrysoperla, Hippodamia, Geocoris	1, 14	0.10	0.7595	1, 14	3.64	0.0648	1, 14	1.33	0.2566

CHAPTER 4

INCREASING ENEMY BIODIVERSITY LEADS TO GREATER FORAGING EFFICIENCY ON TWO PLANT SPECIES

Abstract. Concern over biodiversity loss, especially at higher trophic levels, has led to a surge in studies investigating how changes in natural enemy diversity affect community and ecosystem functioning. These studies have found that increasing enemy diversity can strengthen, weaken, and not affect prey suppression, demonstrating that multi-enemy effects on prey are context-dependent. Here we ask how one factor, plant species identity, influences multi-enemy effects on prey. We focused on two plant species of agricultural importance, potato (*Solanum tuberosum*), and collards (*Brassica oleracea* L.). These species share a common herbivorous pest, the green peach aphid (*Myzus persicae*), but vary in structural and chemical traits that may influence inter-enemy interactions. In a large-scale field experiment, overall prey exploitation varied dramatically among the plant species, with enemies reducing aphid populations by ~94% on potatoes and ~62% on collards. Increasing enemy diversity similarly strengthened aphid suppression on both plants, however, and there was no evidence that plant species identity significantly altered the relationship between enemy diversity and prey suppression. Microcosm experiments revealed that, on both collards and potatoes, multi-enemy effects were subadditive for conspecifics and additive for heterospecifics, indicating functional redundancy and functional complementarity, respectively. Enemy species showed consistent and significant differences in where they foraged on the plants, and enemies in the low diversity treatments tended to spend less time foraging than enemies in the high diversity treatments. These data suggest that increasing enemy

diversity strengthens aphid suppression because interspecific differences in plant space use allow for greater resource partitioning in species-rich communities. Further, these functional benefits of diversity appear to be robust to changes in plant species identity.

INTRODUCTION

Concern over biodiversity loss, especially at higher trophic levels, has led to a surge in studies investigating the ecological consequences of diminishing natural enemy biodiversity. These studies have found positive multi-enemy effects, in which complementary resource use among enemy species strengthens prey suppression (Bogran et al. 2002, Cardinale et al. 2003, Wilby et al. 2005, Snyder et al. 2006), negative multi-enemy effects, in which interspecific interference weakens prey suppression (Rosenheim et al. 1993, Snyder and Ives 2001, Finke and Denno 2004, 2005), and neutral multi-enemy effects, in which increasing enemy diversity has no effect on the strength of prey suppression (Rodriguez and Hawkins 2000, Schmitz and Sokol-Hessner 2002, Aukema and Raffa 2004, Straub and Snyder 2006a).

The variation in multi-enemy effects observed in different systems suggests that the relationship between enemy diversity and prey suppression is context-dependent. This realization has led to a shift in focus from describing the relationship between enemy diversity and prey suppression, to identifying the ecological factors that modify this relationship (Wilby and Thomas 2002, Finke and Denno 2005, Vance-Chalcraft and Soluk 2005, Wilby et al. 2005, Rosenheim and Harmon 2006, Straub and Snyder, in prep). Much of this work has focused on intraguild predation, a negative interaction in which enemy species consume one another in addition to the focal prey species (Polis et

al. 1989). In one study on intraguild predation, the effect of increasing predator diversity on herbivore suppression was shown to vary from negative to neutral, depending on whether or not intraguild predator species were included in the community (Finke and Denno 2005). Interestingly, the identity of the intraguild prey species appears to matter as well. In a recent meta-analysis, multi-enemy effects were most often neutral when the intraguild prey species was a widely foraging predator, but positive when the intraguild prey species was an immobile parasitoid developing within the shared host (Rosenheim and Harmon 2006). Finally, multi-predator effects may also depend on the identity of the shared prey species. Indeed, both theoretical and empirical evidence support the hypothesis that multi-enemy effects are more likely to be neutral when the prey species is a hemimetabolous insect with a simple life cycle, and positive when the prey species is a holometabolous insect with a more complex life cycle (Wilby and Thomas 2002, Wilby et al, 2005).

While there is growing evidence that multi-enemy effects depend on the identity of the predators and prey that are in the community, it is less clear whether variation in plant species identity also modifies multi-enemy effects. Plant waxes and structural complexity have been shown to interfere with the attachment, mobility, and efficiency of enemy species (Kareiva and Sahakian 1990, Eigenbrode et al. 1996, Legrand and Barbosa 2003), and there is evidence that leaf surface structures such as trichomes and domatia can provide refuges from intraguild predation (Agrawal and Karban 1997, Roda et al. 2000, Norton et al. 2001). Further, plant species identity could influence inter-enemy interactions by its direct effect on prey density: increasing prey density has been shown to reduce intraguild predation and aggression among enemies (Peckarsky and

Penton 1985, Lucas et al. 1998, Obrycki et al. 1998, Amarasekare 2003) and strengthen complementary resource use among enemies (Losey and Denno 1998), although there are counterexamples to these patterns (Vance-Chalcraft and Soluk 2005). In sum, these and other multi-trophic studies suggest that plant species identity may often modify multi-enemy effects (Denno et al. 2005). However, few experiments have directly manipulated enemy diversity and plant species identity to test this hypothesis (but see Aquilino et al. 2005).

Understanding how factors such as predator, prey, or plant species identity alter multi-enemy effects requires an understanding of the mechanisms that drive these effects. In contrast to the massive body of literature focusing on intraguild predation (Arim and Marquet 2004, Rosenheim and Harmon 2006), much less work has focused on the mechanisms by which increasing enemy diversity can strengthen prey suppression. Positive multi-enemy effects are collectively referred to as species, niche, or functional complementarity (Loreau et al., Tilman et al. 2001, Casula et al. 2006). Functional complementarity can be divided into two classes of mechanism depending on whether interspecific interactions (other than competition) are involved (Casula et al. 2006). Resource partitioning, which assumes no interspecific interactions, occurs when enemies consume different prey sub-populations. In the extreme case where resource partitioning is perfect, there is no competition between enemy species and enemies are completely additive in their combined effects on prey. At the other extreme, enemies completely overlap in their resource use. These enemies are said to be functionally redundant and would have subadditive effects on prey (Wilby and Thomas 2002, Ives et al. 2005, Casula et al. 2006). Two additional mechanisms that may lead to complementarity

resource use, but involve interspecific interactions, are facilitation and phenotypic niche extension (Casula et al. 2006). Facilitation, also known as synergy and prey-risk enhancement, occurs when one enemy increases the feeding rate of another, and often results from conflicting prey defences (Losey and Denno 1998, Sih et al. 1998). The combined impact of enemy species that facilitate one another is greater than would be predicted by summing their individual impacts, i.e., it is a superadditive process. Finally, phenotypic niche extension occurs when one enemy species causes another to adjust its foraging behavior to include prey that it would be unlikely to eat if foraging with only conspecifics (Bogran et al. 2002, Casula et al. 2006). This can be distinguished from facilitation in that the extending enemy does not consume more prey, just different prey. Under phenotypic niche extension, multi-enemy effects can be additive, which makes this mechanism clearly distinct from facilitation but difficult to distinguish from resource partitioning on the basis of prey consumption alone (Casula 2006).

There were two main objectives of the current study. The first objective was to test the hypothesis that plant species identity mediates multi-enemy effects. This was accomplished by manipulating enemy diversity and plant species identity in a large-scale field experiment. The second objective was to elucidate the mechanism by which increasing enemy diversity enhances prey suppression in our system, with the related goal of understanding how changes in plant species identity may affect the operation of this mechanism. This objective was accomplished by conducting smaller scale greenhouse experiments where we could more easily observe natural enemy behavior. We focused on two plant species of agricultural importance, potatoes (*Solanum tuberosum*), and collards (*Brassica oleracea* L.). These plant species were selected for

study for several reasons. First, a clearer understanding of multi-species interactions on these plants could potentially lead to improved pest management. Second, these plants share a common herbivore species, the green peach aphid, which allowed us to manipulate plant species identity while holding prey species identity constant. Third, collards have simple leaves with a waxy surface, potatoes have pinnately compound leaves with pubescence, and previous work with these two plants has shown that green peach aphids have higher reproductive rates on collards than on potatoes, perhaps because of differences in plant chemistry (Straub and Snyder, pers. observ.). Thus, these plant species differ in numerous traits that may modify multi-enemy effects. Finally, we have observed positive multi-enemy effects on collards (Snyder et al. 2006) and neutral multi-enemy effects on potatoes (Straub and Snyder 2006). Based on this previous work, and on the mass of literature suggesting that multi-enemy effects may become increasingly positive with greater prey density, we predicted positive and neutral multi-enemy effects on collards and potatoes, respectively.

METHODS

Field experiment

The field experiment was conducted at the Washington State University Othello Research Station in southcentral Washington. Our focal prey, the green peach aphid, is an important pest of vegetable crops in Washington (Koss et al. 2005). Locally, a diverse community of enemies attack green peach aphid (for a more detailed description of the enemy community, see Koss et al. 2005, Snyder et al. 2006, Straub and Snyder 2006a). Four of these taxa were used in the experiments reported here: *Aphidius matricariae*,

Nabis spp., *Coccinella septempunctata*, and *Hippodamia convergens*. The predators were field-collected using a D-vac suction sampler (Rincon Vitova, Ventura, California, USA) or by hand and were used within one week of collection. *A. matricariae* was obtained from a commercial insectary (Rincon Vitova, Ventura, California, USA).

For the field experiment, mesocosms were 2 x 2 x 2 m cages with 32 x 32 mesh Lumite screening and a zipper on one side to allow entry (BioQuip, Gardena, California, USA). The bottom edges of the cages were buried under ~20 cm soil to prevent arthropod movement in and out of the cages. Each cage received eight collard or potato plants that were three or four weeks old, respectively. We measured the height (from the first root to the central apical leaf) and the number of nodes (the juncture of each leaf with the stem) of five haphazardly selected collard and potato plants before the experiment began. Collards and potatoes had similar heights (collard: 15.26 ± 0.67 cm; potato: 15.8 ± 1.14 cm) but varied dramatically in the number of nodes (collard: 5.2 ± 0.2 nodes; potato: 121.2 ± 8.67 nodes). While each collard node gave rise to a simple leaf, each potato node gave rise to a pinnately compound leaf with numerous small leaflets. The green peach aphids used in the collard and potato treatments were reared in the field on collards and potatoes, respectively (aphid rearing as in Snyder et al. 2006, Straub et al. 2006a). Approximately 25 aphids were added to each plant and were permitted four days to establish before enemies were introduced. Just before the enemy introduction, we counted the number of aphids on four randomly selected plants in each cage and calculated the mean number of aphids per plant. There were more aphids on collards (21.24 ± 1.042) than on potatoes (5.51 ± 1.01).

Plant species identity (collards, potato) and enemy diversity (low diversity, high diversity) were experimentally manipulated in a completely randomized 2 x 2 factorial design, yielding four treatments: collard, low diversity (n = 12); collard, high diversity (n = 5); potato, low diversity (n = 12); potato, high diversity (n = 5). We also included a no-enemy control treatment: collard control (n = 5); potato control (n = 5). In the low diversity treatments, each of the four enemy species was replicated three times in monoculture (4 species x 3 replicates/species = 12 low diversity replicates on each plant species). The high diversity treatments were represented by a single composition that included all four enemy species. High diversity treatments were replicated five times on each plant species, although one collard replicate was discarded because the enemies escaped through a tear in the cage screening. We used an enemy density of 36 individuals per cage, which is well within the range of densities found in local agricultural fields (Snyder et al. 2006). As in our previous studies (Snyder et al. 2006, Straub and Snyder 2006a), this predator density was held constant across diversity treatments with a substitutive experimental design, so that low and high diversity communities received 36 and nine individuals of each species, respectively. Further, the potential for sampling effects (Huston 1997) was minimized because the relative proportion of each species was equal in the low and high diversity treatments. The strengths and weaknesses of this experimental approach have been discussed at length elsewhere (Connolly 1998, Jolliffe 2000, Griffen 2006, Straub and Snyder 2006b).

The experiment was terminated after 17 days, which was long enough to allow for 1 parasitoid generation (adult to pupae). Aphids and parasitoid pupae (mummies) were

counted on four randomly selected plants from each cage. The remaining predators were collected by hand on the following day.

Greenhouse experiments

To investigate the mechanism by which diversity strengthens aphid suppression in our system, we conducted companion experiments using the same assemblage of enemies but in 45 L (10 gallon) aquaria where we could easily observe predator behavior. For logistical reasons, we were unable to manipulate plant species identity within a single experiment. Thus, we conducted two separate experiments, one on collards and one on potatoes. Each microcosm housed a single potted plant that was ~ 3 weeks old. For the collard experiment, 200 green peach aphids were added and allowed to establish for 48 hours before the enemy introduction. For the potato experiment, 150 aphids were added 96 hours before enemy introduction. We noticed considerable variation across replicates in the number of aphids that had established on potatoes, so we recorded the initial aphid number just prior to enemy release and included this number as a covariate in the analyses of green peach aphids on potato. Both experiments were terminated at 72 hours, at which time we removed all enemies and counted the remaining aphids. Seven days later we counted the mummies, and the mummies were subtracted from the aphid data to account for the aphids that were killed by parasitoids.

In both microcosm experiments, there were four treatments: no-enemy control ($n = 3$), low density-low diversity ($n = 12$), low diversity ($n = 12$), and high diversity ($n = 5$), although one replicate was lost from the high diversity treatment in the collard experiment because several enemies were able to escape due to a poorly fitted aquarium

lid. In the low density-low diversity treatment (LDLD), each species was replicated three times in monoculture at a density of two enemies/microcosm. In the low diversity treatment (LD), each species was replicated three times at a density of eight enemies/microcosm. The high diversity treatment (HD) consisted of a single enemy composition that included all four enemy species, each of which was represented by two individuals for a total of eight enemies/microcosm. As with the field experiment, this experimental design allowed us to test for diversity effects without the confounding effects of density by comparing the strength of aphid suppression in LD and HD. In addition, by comparing the mean per capita interaction strength of enemies in LD and HD to the mean per capita interaction strength of enemies in LDLD, we were able to determine if conspecific and heterospecific multi-enemy effects were subadditive ($<$ LDLD), additive ($=$ LDLD), or superadditive ($>$ LDLD). Subadditive multi-enemy effects would indicate functional redundancy among enemies, most likely driven by strong competition. An implicit assumption of resource partitioning, phenotypic niche extension and facilitation is that greater functional redundancy exists in low than high diversity communities. Additive multi-enemy effects would indicate functional complementarity driven by resource partitioning and/or phenotypic niche extension. Finally, superadditive multi-enemy effects would indicate functional complementarity driven by facilitation. The per capita interaction strength for each replicate in the three natural enemy treatments was calculated according to Wootton (1997): $\ln(N_{ea} / N_{ep})/E$, where N = final aphid density, ea = enemies absent, ep = enemies present, and E = enemy density. We used the mean aphid abundance of the no-predator controls for the N_{ea} term.

Measures of enemy behavior were taken throughout the experiments to assess whether complementary space use occurs among the natural enemies. For aphid enemies, interspecific variation in space use could serve as the functional foundation for resource partitioning, facilitation, and phenotypic niche extension (Chang 1996, Losey and Denno 1998, Cardinale et al. 2006). For instance, in an example of resource partitioning, additive aphid suppression among potential intraguild predators has been attributed to interspecific variation in plant space use (Chang 1996). In an example of facilitation, aphids escaping from plant-foraging coccinellids have been shown to drop to the ground where they are eaten by ground-foraging beetles (Losey and Denno 1998). Finally, larger, behaviorally dominant coccinellids can cause smaller coccinellids to forage in sub-optimal places on the plant where they would not forage otherwise (Cardinale et al. 2006). This behavioral shift is a form of phenotypic niche extension and could potentially lead to greater aphid suppression in our system, which includes relatively large (*Coccinella septempunctata*; ~ 15 mg dry mass, n = 5) and small (*Hippodamia convergens*; ~ 5 mg dry mass, n = 10) coccinellid species.

On 12 occasions, each replicate from LD and HD was observed for 30 seconds. Scan samples of each replicate were separated by two or more hours, allowing ample time for the enemies to redistribute themselves between observations. Thus, each of these samples is treated as an independent observation in the analyses. During each observation, we recorded the proportion of each enemy species that was on the plant. For those predators that were on the plant, we recorded their location as stem, leaf-edge, or leaf-core. Enemies that were on leaves but more than 1 cm from the nearest leaf-edge were recorded as being in the leaf-core.

We addressed three questions with these behavioral data: 1) Do enemy species show significant variation in where they forage on the plant, as would be expected if they partition plant space? 2) Does the distribution of enemy species across plant space change with increasing diversity, as might be expected under phenotypic niche extension? 3) Do a greater proportion of enemies occur on the plants in HD than LD, as might be expected if increasing diversity leads to less competition (and less functional redundancy)? Here we assume that the time spent on the plant is proportional to the time spent foraging.

Data analyses

In our experimental design, there are four enemy compositions in the low diversity treatments (i.e., each enemy species in monoculture), but only one composition in the high diversity treatments (i.e., all four species together). As a consequence, the variance in aphid abundance was significantly greater in the low diversity treatments, violating the equal variance assumption of parametric ANOVA. Thus, the aphid data were rank-transformed and analyzed by nonparametric ANOVAs and planned contrasts (Zar 1999). For the field experiment, the effects of plant species identity, enemy diversity, and their interaction were investigated. The interaction between plant species identity and enemies (present versus absent) on aphid abundance was also tested. For the greenhouse experiments, nonparametric ANOVA was followed by planned contrasts to determine if there was an overall effect of enemies (no-predator control vs. the mean of LDLD, LD, HD) and an effect of increasing diversity (LD vs. HD). Nonparametric ANOVA on mean per capita interaction strengths was followed by a series of planned contrasts (LDLD vs. LD, LDLD vs. HD, and LD vs. HD). *t* - tests and Chi square tests

were used to compare enemy space use across species and diversity treatments. All analyses were conducted in SAS v. 8.02 (SAS Institute, Inc., 2003).

RESULTS

Field experiment

Aphid abundance

At the beginning of the experiment, just before enemies were released, there were significantly more aphids on collards than on potato (plant main effect: $F_{1,37} = 111.13$, $P < 0.0001$) but there was no difference among the three enemy treatments (no-enemy control, low diversity, high diversity) for either collards ($F_{2,17} = 0.03$, $P = 0.97$) or potato ($F_{2,18} = 0.03$, $P = 0.99$). At the end of the experiment, there were still more aphids on collards than on potatoes (plant main effect: $F_{1,37} = 35.11$, $P < 0.0001$). Enemies significantly suppressed aphid populations (enemy main effect: $F_{1,37} = 37.36$, $P < 0.0001$). However, enemies were more effective on potatoes than on collards (plant x enemy interaction: $F_{1,37} = 4.34$, $P = 0.044$, Fig. 1a), and caused a 94.30% and 61.76% reduction in aphids on potatoes and collards, respectively. Increasing enemy diversity led to greater aphid suppression on both plant species (diversity main effect: $F_{1,29} = 5.85$, $P = 0.022$), and there was no evidence that plant species identity modified the effect of enemy diversity on aphid suppression (plant x diversity interaction: $F_{1,29} = 0.03$, $P = 0.873$, Fig. 1a).

Enemy abundance

Increasing natural enemy diversity had contrasting effects on predator and parasitoid fitness, leading to greater predator survivorship ($F_{1,23} = 4.59, P = 0.043$, Fig. 1b) and lower per capita mummy production by parasitoids ($F_{1,11} = 60.4, P < 0.0001$, Fig. 1c). Plant main effects and plant x diversity interactions were not significant ($P > 0.05$, Fig. 1b, c).

Greenhouse experiments

Aphid abundance

There was significant variation among the four experimental treatments for both collards ($F_{3,27} = 8.13, P = 0.0005$, Fig. 2a) and potatoes ($F_{4,27} = 11.38, P < 0.0001$, Fig. 2c). Planned contrasts showed that enemies suppressed aphid populations (no-predator control vs. the mean of all enemy treatments; collards: $F_{1,27} = 15.52, P = 0.0005$; potatoes: $F_{1,27} = 14.95, P = 0.0006$) and that increasing natural enemy diversity led to greater aphid suppression (LD vs. HD; collards: $F_{1,27} = 8.46, P = 0.0072$, Fig. 2a; potatoes: $F_{1,27} = 6.78, P = 0.015$; Fig. 2c). Per capita interaction strength varied among the three enemy treatments (collards: $F_{2,25} = 8.04, P = 0.0002$, Fig. 2b; potatoes: $F_{2,25} = 6.13, P = 0.020$, Fig. 2d). Planned contrasts showed that the mean per capita interaction strength was greater for enemies in LDLD than for enemies in LD (collards: $F_{1,25} = 14.41, P = 0.0008$; potatoes: $F_{1,25} = 8.19, P = 0.0084$), indicating that conspecific multi-enemy effects were subadditive. There was no difference between LDLD and HD (collards: $F_{1,25} = 0.02, P = 0.90$; potatoes: $F_{1,25} = 0.15, P = 0.70$), indicating that heterospecific multi-enemy effects were additive. The mean per capita interaction strength was greater for enemies in HD than LD, although the difference only neared

statistical significance on potatoes (collards: $F_{1,25} = 6.52$, $P = 0.017$; potatoes: $F_{1,25} = 3.17$, $P = 0.087$).

Enemy behavior

On collards, 43.70 %, 38.66 %, and 17.65 % of enemy observations were from the stem, leaf-edge, and leaf-core, respectively. There was significant variation among species in the relative frequency with which they were observed in these three locations ($\chi^2 = 47.01$, d.f. = 6, $P < 0.0001$; Fig. 3a). Pairwise comparisons revealed that, with the exception of *Coccinella* and *Hippodamia*, all species significantly differed from one another (Table 1). There was no effect of increasing diversity on where enemies were located on plants (Table 2), providing no evidence for phenotypic niche extension across plant space.

A greater proportion of *Coccinella* ($t_5 = -3.63$, $P = 0.015$) and *Hippodamia* ($t_5 = -3.40$, $P = 0.019$) were observed on plants in HD than LD. There was no effect of diversity on the proportion of *Nabis* observed on plants ($t_5 = 1.29$, $P = 0.254$) and a smaller proportion of *Aphidius* was observed on plants in HD than LD ($t_5 = 2.66$, $P = 0.045$). The conflicting responses of enemies to increasing diversity led to no overall effect of enemy diversity on the mean proportion of total enemies observed on the plant ($t_{14} = -1.30$, $P = 0.214$; Fig. 3b).

On potatoes, 17.39 %, 60.33 %, and 22.28 % of predator observations were from the stem, leaf-edge, and leaf-core, respectively. There was significant variation among species in the relative frequency with which they were observed in these three locations ($\chi^2 = 23.32$, d.f. = 6, $P = 0.001$; Fig. 3c). Pairwise comparisons revealed that, with the

exception of *Nabis*, which was not significantly different from any species, all other species significantly differed from one another (Table 1). Once again, there was no effect of increasing diversity on where enemies were located (Table 2), providing no evidence for phenotypic niche extension across plant space.

There was a trend toward proportionately more enemies on plants in the HD than LD for all enemy species (but $P > 0.05$ for all four species), leading to a greater total proportion of enemies observed on plants in HD than LD ($t_{15} = -2.61$, $P = 0.020$; Fig. 3d).

DISCUSSION

Variation in plant species identity affected aphid reproductive rates and the strength of aphid suppression by enemies (Fig. 1a). However, the hypothesis that positive multi-enemy effects would be observed on collards, but not on potatoes, was rejected. Instead, increasing enemy diversity strengthened herbivore suppression on both collards and potatoes (Fig. 1a). These results demonstrate that the functional complementarity observed among enemies was robust to changes in plant species identity, and suggest that variation plant species identity cannot, by itself, explain why positive multi-enemy effects were not observed in our earlier work on potatoes (Straub and Snyder 2006a).

In the microcosm experiments, we found that increasing enemy diversity strengthened aphid suppression on both collards and potatoes (Fig. 2a, c). This reinforces the conclusion that the effects of enemy diversity on prey suppression were not altered by plant species identity, and demonstrates that the functional complementarity observed in the field also occurs on a much smaller spatiotemporal scale. By manipulating both predator diversity and density, we found that conspecific multi-predator effects were sub-

additive, indicating functional redundancy within species, while heterospecific multi-predator effects were additive, indicating functional complementarity among species (Fig 2b, d). To further investigate this functional complementarity, we examined natural enemy space use. There was significant variation among enemy species in where they were located on the plant (Fig. 3a, c, Table 1), and plant space partitioning among enemy species could serve as the functional foundation for resource partitioning (Chang 1996), phenotypic niche extension (Bogran et al. 2002) and facilitation (Losey and Denno 1998). Facilitation is a superadditive process in which one predator species increases the foraging efficiency of a second species (Sih et al. 1998). Our finding that heterospecific multi-predator effects were additive is inconsistent with facilitation, although we cannot rule out the possibility that interference among one subset of species counteracted facilitation among a different subset and led to a net additive effect of increasing enemy diversity. Phenotypic niche extension could have led to additive multi-enemy effects among heterospecifics if one species caused another species to consume a sub-population of prey that it did not consume when foraging with conspecifics. The observation that enemy diversity had no effect on where individual species occurred on the plants suggests that phenotypic niche extension, at least across plant space, did not occur (Table 2). Thus, the results of the microcosm experiments suggest that the observed functional complementarity most likely results from resource partitioning, and not from mechanisms that require interspecific interactions. However, the absence of evidence for facilitation and phenotypic niche extension should not be taken as unequivocal evidence for their absence, and our rejection of these mechanisms is tentative.

In the absence of interspecific interactions, greater plant space partitioning among heterospecifics could have led to additive aphid suppression in two ways. First, it may have reduced exploitation (or scramble) competition if the enemy species consumed different sub-populations of prey that were found on different parts of the plant (Casula et al. 2006). Second, it is possible that greater plant space partitioning reduced interference (or contest) competition by reducing enemy-enemy encounter rates. Note that this latter form of competition is mediated by behavioral (or chemical) interactions and does not require that the predators actually feed on different sub-populations of prey within a plant. Exploitation and interference competition are not mutually exclusive, and future work that closely focuses on prey-use patterns and inter-enemy behavioral (and chemical) interactions across plant space will be needed to assess the relative importance of these two mechanisms. Regardless of the exact mechanism, the behavioral observations suggest that increasing enemy diversity strengthens aphid suppression because interspecific differences in plant space use allow for greater resource partitioning and more efficient resource use at the community level.

While variation in plant species identity did not alter the relationship between enemy diversity and prey suppression, interspecific differences in plant architecture did affect enemy space use. Collards have a few large simple leaves, while potatoes have many pinnately compound leaves with small leaflets. As a consequence, the surface area of a collard plant is more evenly divided among the stem, leaf-edge, and leaf-core, while most of the surface area of a potato plant occurs at the edges of leaflets. This variation in plant architecture allowed for greater space partitioning on collards than on potatoes (Fig. 3a, c, Table 1). At least in part, the greater space partitioning on collards can be explained

by the fact that, compared with potatoes, *Aphidius* spent relatively more time in the leaf-core on collards while *Coccinella* and *Hippodamia* spent relatively less time in the leaf-core on collards. This interspecific difference in leaf-core use may have been exaggerated on collards because collards have relatively more leaf-core, attachment to the leaf-core of waxy plants is difficult, and the problem of attachment is greater for larger, heavier-bodied enemies (Grevstad and Klepetka 1992, Eigenbrode et al. 1996).

The greater space partitioning observed on collards suggests that there should also have been greater resource partitioning on collards. However, if resource partitioning was greater on collards, increasing enemy diversity would have strengthened aphid suppression more on collards than on potatoes. This did not happen (Fig. 1a). Several observations of enemy behavior may help to resolve this problem. First, increasing diversity tended to cause all four enemy species to spend more time on potato plants, indicating that intraspecific competition exceeded interspecific competition for all species on potatoes (Fig. 3d). In contrast, increasing enemy diversity on collards led to proportionately more *Coccinella* and *Hippodamia* on the plant, and proportionately fewer *Aphidius* and *Nabis* on the plant (Fig 3d). This suggests that *Coccinella* and *Hippodamia* experienced stronger intraspecific competition on collards while *Aphidius* and *Nabis* experienced stronger interspecific competition. Consistent with this hypothesis, we observed the larger coccinellids encountering *Aphidius* and *Nabis* and scaring them from the plant on several occasions. We suggest that these antagonistic encounters were more frequent on collards than on potatoes because of differences in plant architecture. Specifically, because collards have relatively more leaf-core and less leaf-edge, they have a smaller perimeter than do potatoes. Coccinellid traffic along the perimeter of collards

was particularly high, in part because the coccinellids had difficulty accessing the leaf-core of collards (Fig. 3a), and it appeared that this traffic created a barrier to entry that prevented *Aphidius* and *Nabis* from gaining access to the collards. Thus, our observations suggest that multi-enemy interactions were influenced by plant species identity (Fig. 3b, d), and that the greater opportunity for resource partitioning on collards may be counteracted by greater interspecific interference on collards, leading to *net* effects of increasing enemy diversity that were similar on the two plant species (Fig. 1a).

Three other differences between collards and potatoes also warrant discussion. First, aphids reproduced at a higher rate on collards than on potatoes (Fig 1a, no-enemy control line), indicating that collards are a higher quality host. While previous studies have suggested that prey density may modify multi-enemy effects (e.g., Peckarsky and Penton 1985, Losey and Denno 1998, Lucas et al. 1998, Amarasekare 2003, Griffen 2006), our results are consistent with other studies showing that multi-enemy effects are independent of prey density (Vance-Chalcraft and Soluk 2005). Second, enemies were more effective on potatoes than on collards (Fig 1a). Collards have more leaf-core area than potatoes, and 46% of aphids occurred in the leaf-core on collards compared with only ~11% on potatoes (estimates based on no-enemy controls in the greenhouse experiments). Meanwhile, behavioral observations suggest that the leaf-core is the most difficult place to access for all enemies (Fig. 3a, c), perhaps because attachment is difficult (Grevstad and Klepetka 1992, Eigenbrode et al. 1996). Thus, the most likely explanation for enemies being more effective on potatoes is that collards provide a larger spatial refuge for aphids. Finally, an important difference between collards and potatoes involves the potential benefits of enemy diversity in these systems. In the field

experiment, the mean difference between the low and high diversity treatments was ~6 aphids on potatoes and ~200 aphids on collards. So while the *relative* effect of increasing enemy diversity on aphid suppression does not vary with plant species (Fig. 1a), the *absolute* effect of increasing predator diversity is considerably larger on collards. Taken together, these three differences between collards and potatoes suggest that, from an applied perspective, biological control may be a more effective pest management strategy in potatoes because natural enemies can access a greater proportion of the aphids on this plant. However, the functional benefits of conserving enemy diversity appear to be far greater in collards because this crop supports higher densities of aphids and has more to gain from stronger pest suppression.

In summary, despite considerable differences in plant structure and spatiotemporal scale, we have found that increasing diversity within the natural enemy assemblage examined here consistently leads to greater aphid suppression. This functional complementarity may result from interspecific variation in plant space use, and this study makes an important first step toward elucidating at least one mechanism by which enemy diversity can strengthen prey suppression. However, identifying the functional trait combinations that promote positive, negative, and neutral diversity effects still remains an important challenge, and further progress on this front is needed to improve our ability to effectively manage natural and agricultural ecosystems.

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Table 1. Pairwise comparisons of species distributions (stem, leaf-edge, leaf-core)

Pairwise comparison	Collards			Pairwise comparison	Potato		
	df	χ^2	<i>P</i>		df	χ^2	<i>P</i>
<i>Aphidius</i> , <i>Nabis</i>	2	8.737	0.0127	<i>Aphidius</i> , <i>Nabis</i>	2	3.977	0.1369
<i>Aphidius</i> , <i>Coccinella</i>	2	28.729	<0.0001	<i>Aphidius</i> , <i>Coccinella</i>	2	8.528	0.0141
<i>Aphidius</i> , <i>Hippodamia</i>	2	28.134	<0.0001	<i>Aphidius</i> , <i>Hippodamia</i>	2	15.717	0.0004
<i>Nabis</i> , <i>Coccinella</i>	2	12.451	0.0020	<i>Nabis</i> , <i>Coccinella</i>	2	3.269	0.1951
<i>Nabis</i> , <i>Hippodamia</i>	2	11.221	0.0037	<i>Nabis</i> , <i>Hippodamia</i>	2	5.192	0.0746
<i>Coccinella</i> , <i>Hippodamia</i>	2	3.346	0.1877	<i>Coccinella</i> , <i>Hippodamia</i>	2	6.229	0.0444

Table 2. Effect of diversity on the distribution of each species (stem, leaf-edge, leaf-core)

Species	Collards			Species	Potato		
	df	χ^2	<i>P</i>		df	χ^2	<i>P</i>
<i>Aphidius</i>	2	1.919	0.3831	<i>Aphidius</i>	2	1.897	0.3873
<i>Nabis</i>	2	0.930	0.6282	<i>Nabis</i>	2	3.115	0.2107
<i>Coccinella</i>	2	1.018	0.6013	<i>Coccinella</i>	2	0.9338	0.6270
<i>Hippodamia</i>	2	2.120	0.3464	<i>Hippodamia</i>	2	2.656	0.2656

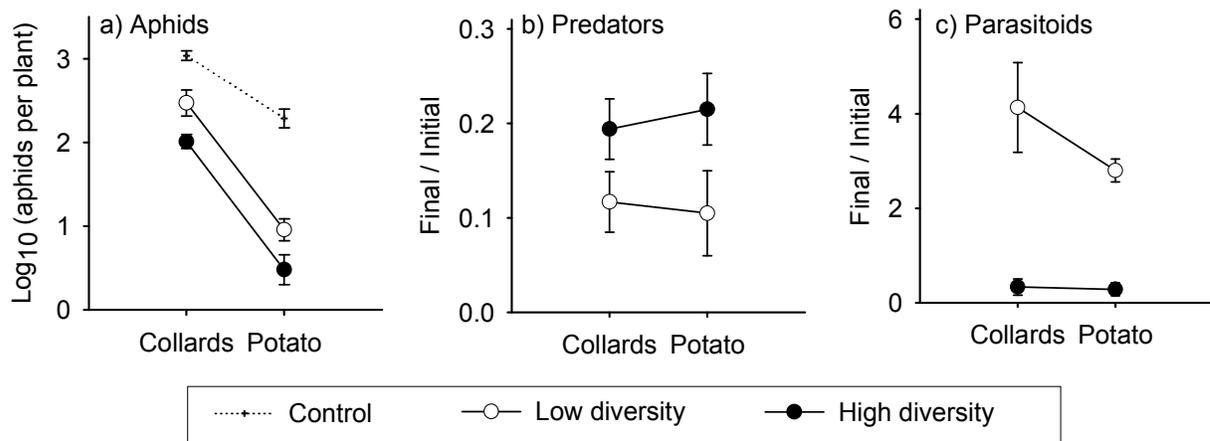


FIG. 1. Results of the field experiment. a) Aphid abundance. Aphids reproduced at a higher rate on collards than on potatoes, increasing enemy diversity led to greater aphid suppression on both plant species, and enemies had a greater impact on aphids on potatoes than on collards. b) Predator abundance. A greater proportion of predators (final abundance/initial abundance) survived in high than in low diversity communities. c) Parasitoid abundance. Lower per capita mummy production (final parasitoid pupal abundance/initial adult parasitoid abundance) was observed in high than in low diversity communities. Data are means \pm 1 s.e.

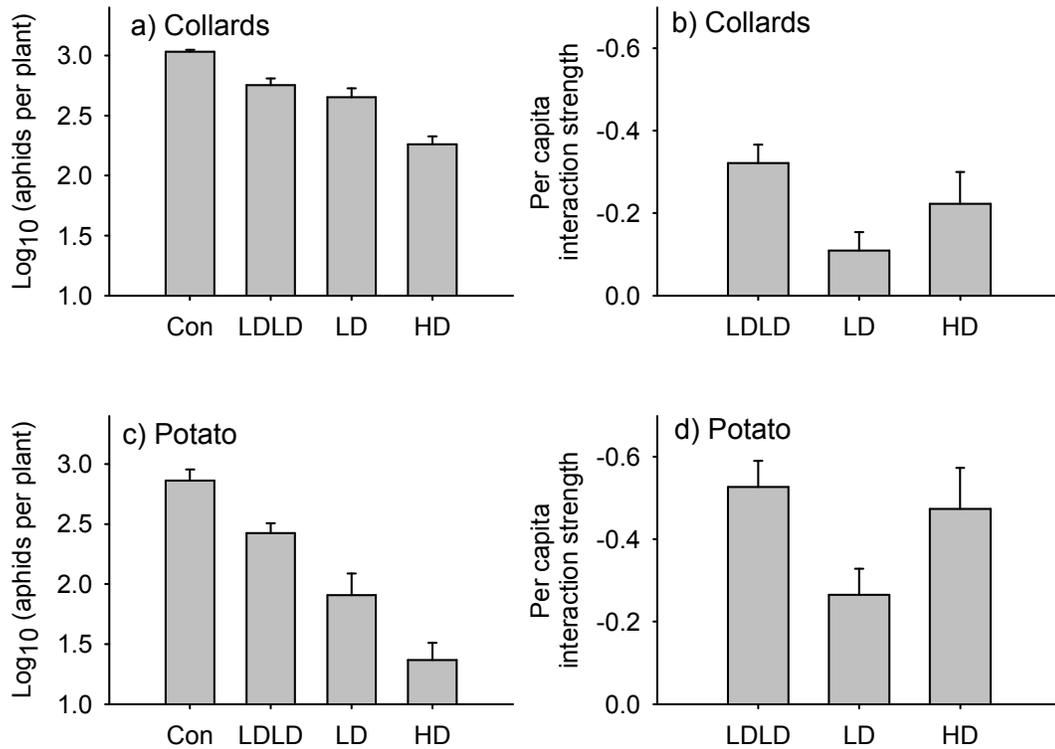


FIG. 2. Aphid suppression in the greenhouse experiments. a, c) Aphid abundance. Enemies suppressed aphid populations and increasing diversity strengthened aphid suppression on both plant species. b, d) Mean per capita interaction strengths of the three natural enemy treatments. Multi-enemy impacts were subadditive for conspecifics ($LD < LDLD$) and additive for heterospecifics ($HD = LDLD$) on both plant species. Con = no-enemy control, LDLD = low density-low diversity, LD = low diversity, HD = high diversity. Data are means \pm 1 s.e.

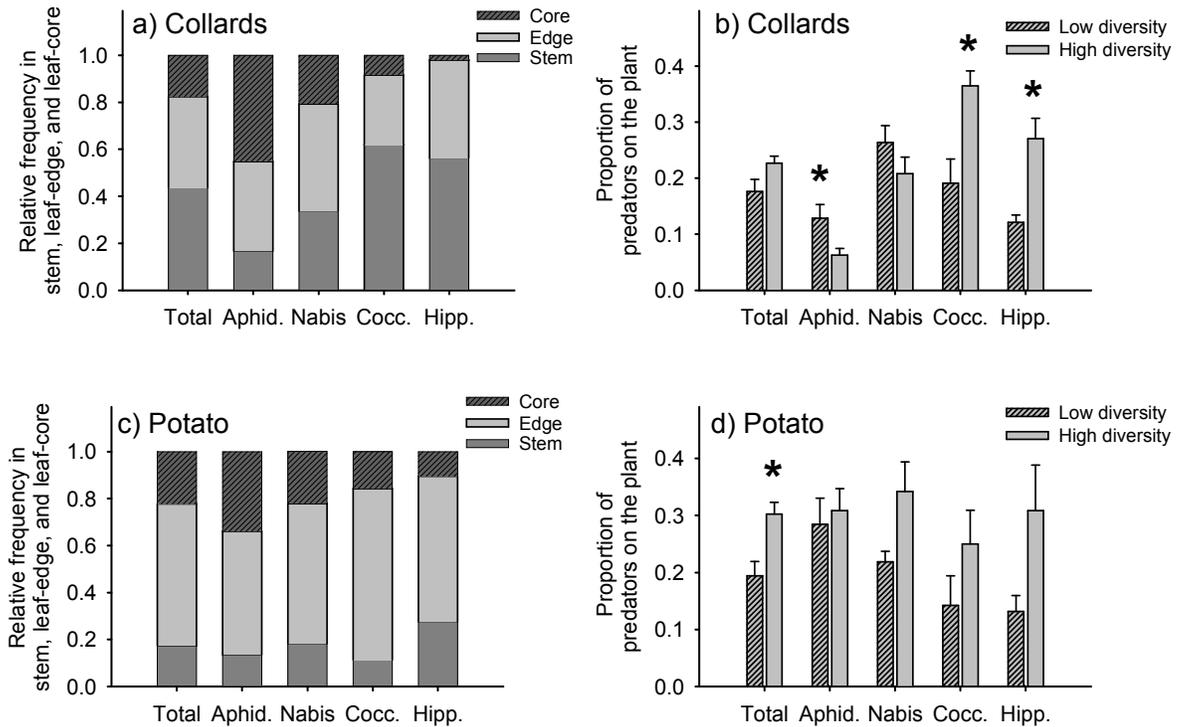


FIG. 3. Enemy behavior in the greenhouse experiments. a, c) For each species, the relative frequency of observations on the stem, leaf-edge, and leaf-core. Species distributions significantly differed from one another indicating plant space partitioning among species. Mean proportion of enemies observed on (versus off) the plant in low and high diversity treatments. b, d) *Coccinella* and *Hippodamia* spent proportionately more time on both collard and potato plants when in diverse communities, while *Aphidius* and *Nabis* responses varied with plant species. Asterisks indicate significant differences ($P < 0.05$). Total = all four enemy species combined, Aphid. = *Aphidius*, Nabis = *Nabis*, Cocc. = *Coccinella*, Hipp. = *Hippodamia*. Data are means \pm 1 s.e.

CONCLUSIONS

Agricultural pest suppression is a valuable ecosystem service that may be enhanced by the conservation of natural enemy species. However, it is unclear how conserving natural enemy diversity *per se* affects the biological control of pests, because few studies have attempted to distinguish between the effects of enemy abundance, identity, composition, and diversity. My work demonstrates how an experimental approach traditionally employed by ecosystem ecologists may be used to distinguish between these effects and isolate the effects of enemy diversity on herbivore suppression.

In the first study, I controlled or minimized the effects of species abundance, composition, and identity to isolate the effect of enemy diversity *per se* (i.e., species richness) on the strength of aphid suppression. I found that increasing enemy diversity had no impact on aphid suppression, indicating that the net effects of intraspecific and interspecific enemy interactions on aphid suppression were equal. However, I did find strong species identity effects, indicating that the conservation of a few key enemy species may be a more effective strategy than targeting enemy biodiversity more broadly.

In my second study, I manipulated enemy diversity as before but also replicated individual species compositions in the high diversity treatments, which I had not done in the first study. This enabled me to also examine species composition effects. I found strong effects of species composition on herbivore suppression. Further, the effect of increasing enemy diversity varied from positive to negative depending upon the particular composition of enemy species that was examined. This result suggests that variation in species composition across systems could explain differences in the

relationship between enemy diversity and herbivore suppression observed in different studies.

In my third study, I continued to explore the ecological factors that may alter the relationship between enemy diversity and herbivore suppression. Here I focused on the role of plant species identity in modifying multi-enemy effects, because little is known about how changes at the first trophic level affect multi-enemy interactions, and because previous work had suggested that multi-enemy effects may strengthen aphid suppression on collards but have no effect on aphid suppression on potatoes. Despite considerable differences between collards and potatoes in plant structure, I found that increasing enemy diversity strengthened aphid suppression on both plant species. With the enemy assemblage examined here, conspecific multi-enemy effects were subadditive, indicating functional redundancy within species, while heterospecific multi-enemy effects were additive, indicating functional diversity among species. Closer inspection showed that plant space partitioning among enemy species may allow for greater resource partitioning, leading to more efficient aphid exploitation with increasing enemy diversity. While multi-enemy effects were positive on both collards and potatoes, aphid reproductive rates were much higher on collards. As a consequence, the stronger pest suppression provided by the diverse enemy assemblage led to a larger reduction in aphids on collards than on potatoes. This result suggests that the value of enemy diversity will be far greater in collard than in potato agroecosystems, and is in agreement with our earlier conclusion that the conservation of a few key enemy species may be sufficient for effective biological control in potatoes.

In summary, this body of work clearly demonstrates that changes in enemy species identity, composition, and/or diversity all can alter the strength of herbivore suppression. Further, it appears that a general relationship between enemy diversity and prey suppression may not exist. Instead, multi-enemy effects on prey depend on various ecological factors, and these factors may be intrinsic (e.g., species composition) or extrinsic (e.g., plant species identity) to the enemy community. Identifying the factors that promote positive, negative, and neutral multi-enemy effects, all of which have been demonstrated here, still remains an important challenge. Further progress on this front is needed to improve our ability to effectively manage natural and agricultural ecosystems.