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Coccinellids in diverse communities: which niche fits?

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Abstract

Predaceous lady beetles (Coleoptera: Coccinellidae) are a well-studied group of consumers that can yield insight into relationships among interspecific niche differences, species richness, and prey consumption. In various studies, sympatric lady beetles differ in habitat use at the scales of landscapes, single agricultural fields, and single plants. Species also differ in their seasonal and diel activity patterns. These spatiotemporal differences in habitat use should lead to complementary impacts on prey, by encouraging different predator species to attack different subsets of the prey population. This in turn should lead to stronger biological control at higher predator diversity levels. Indeed, experimental manipulations of predator species richness in communities that include coccinellids have generally revealed stronger prey suppression with greater predator biodiversity. In these experimental studies, lady beetles sometimes filled unique niches as particularly voracious predators, and often also complemented or facilitated prey capture by other species. Intraguild predation was rarely found to be a strongly disruptive force, perhaps because spatiotemporal niche differences reduced encounters among species. In summary, coccinellid species both respond to and affect their communities in unique ways, generally to the benefit of herbivore suppression. Thus, the best niche fit for coccinellids may be that of a complement to other species, contributing to improved biological control with greater predator biodiversity.

Keywords: niche partitioning, facilitation, intraguild predation, biodiversity, Coccinellidae, aphid

1. Introduction

The earth hosts a vast number of different species, and ecologists have long wondered how so many species are able to coexist. Early thinking centered on the concept of the “niche”. The term niche, as used by early ecologists, had two meanings (Chase and Leibold, 2003). Grinnell (1917) used this term to refer to the set of environmental conditions that allow a species to exist. This usage focuses on the impact of the environment on a species, and is sometimes referred to as the “Grinnellian” niche. In contrast, Elton (1927) defined a species’ niche by the resources it consumes. This second usage focuses on how a species impacts its resources, and can be called the “Eltonian” niche. However, it is clear from their writings both that Grinnell was aware of the importance of trophic connections among species, and that Elton knew that the environment also impacts a species’ range (Grinnell, 1917; Elton, 1927). Thus, while the distinction between Grinnellian and Eltonian niches is useful for discussing these two perspectives, of course in reality there are reciprocal impacts between the organism and its environment (Chase and Leibold, 2003). Classic experimental work by Gause (1936) demonstrated that no two species with identical resource requirements could persist indefinitely without one species out-competing the other. Hutchinson (1957, 1959) proposed that niches could be defined as n-dimensional hypervolumes, with this niche space defined by species trait-value or environmental-requirement axes; this combined the Grinnellian and Eltonian perspectives, and coexisting species would be expected to substantially differ along at least one defining axis. Early-on the niche became a foundational concept in ecology (Schoener, 1974), leading to a flurry of studies where many species traits were measured and used to infer the niche differences that allowed species to coexist (e.g., MacArthur, 1958; Rand, 1964).

The niche concept fell from favor for a time, with critics citing the lack of clear null hypotheses and poor statistical rigor of many niche studies (Strong et al., 1979; Simberloff and Boecklen, 1981; Lewin, 1983). However, the niche has recently re-emerged as a topic of interest. This conceptual resurgence has been triggered in large part by the growing body of experiments on the relationship between biodiversity and ecosystem functioning. These studies generally manipulate species richness and then measure resulting effects on community-wide resource consumption, biomass, or other community processes (Hooper et al., 2005). A clear pattern resulting from these studies, across trophic levels and community types, is that overall resource use generally increases with greater consumer biodiversity (Cardinale et al., 2006). This pattern is generally attributed to the benefits of combining species that occupy different niches, although this mechanism has been surprisingly difficult to demonstrate (Finke and Snyder, 2008). If there is a similar positive relationship between predator biodiversity and biocontrol, increasing the number of natural enemy species will improve pest control (Snyder et al., 2005; Ives et al., 2005). However, it has been suggested that predator communities might diverge from this larger trend. This is because predators often feed on one another in addition to herbivorous prey (Polis et al., 1989), and strong intraguild predation could instead lead to a weakening of herbivore suppression with greater predator biodiversity (Finke and Denno, 2004). Only a better mechanistic understanding of predatory diversity effects will resolve the controversy over whether greater predator biodiversity generally strengthens or weakens herbivore suppression, or if indeed there is a general pattern at all (Straub et al., 2008).

Research on predatory lady beetles (Coleoptera: Coccinellidae) has played a central role in the development of all of the ideas discussed above. Coccinellids often co-occur with a taxonomically diverse group of other predator species (Hagen and van den Bosch, 1968; Root, 1973; Wheeler, 1977; Frazier et al., 1981; Ekbom, 1994), raising the potential for intense competition for prey. Ecological differences among these predators could lead to resource-niche partitioning, and thus a positive relationship between predator biodiversity and herbivore suppression (Finke and Snyder, 2008). At the same time, coccinellids have often been implicated in intraguild predation and other forms of interference competition (Rosenheim et al., 1995; Lucas, 2005; Rosenheim and Harmon, 2006; Snyder and Ives, 2007; Pell et al., 2008; Weber and Lundgren, 2009; Seagraves, 2009, this issue), which could lead instead to a negative relationship between biodiversity and herbivore suppression (Ives et al., 2005). Thus, a clearer understanding of coccinellid ecology may help resolve the nature of the relationship between predator diversity and herbivore suppression.

In this review I first describe the key, and generally underappreciated, role that studies of coccinellids have played in the initial development of the niche concept. Next, I review research on the impacts of the environment on coccinellid diversity and distributions. I then review the growing number of studies where diversity has been manipulated within coccinellid communities, with the goal of revealing the impact of predator biodiversity on herbivore suppression. Most of this second group of studies have also examined the mechanistic basis of biodiversity's role in strengthening or, rarely, weakening herbivore suppression. Of course, studies undertaken from the perspective of resource-requirement impacts on predator diversity often yield insight into trophic interactions, and those examining the resource-exploitation impacts of diverse predator communities on their prey resources often yield insight into the importance of habitat-use differences among species. Several coccinellids are prominent invasive species, and the ecological impacts of these species lend further insight into niche relationships in predator communities. Finally, I discuss similarities and differences in studies examining resource-requirement impacts on predator diversity versus resource-exploitation impacts of predator diversity, summarize mechanisms that lead to niche partitioning, and extrapolate the implications of the research-to-date for the use of coccinellids in biological control.

2. Lady beetles and the early development of the niche concept

The first use of the term niche in an ecological context is often attributed to Grinnell (1917). However, Gaffney (1975) pointed out that the first usage in print actually traces back to Johnson (1910) and his epic monograph on lady beetle color-morph evolution. The section of Johnson's monograph addressing niche differences is relatively short (< 1 page in total), but nicely lays out several key concepts developed later in greater detail, and to greater acclaim, by others. This section of Johnson's monograph opens:

> "*One expects the different species in a region to occupy different niches in the environment. This at least is a corollary of the current belief that every species is as common as it can be, its numbers being limited only by its food-supply, a belief which is a result of the strong Malthusian leanings of Darwin.*" (Johnson 1910, page 87)

That is, resource competition among coccinellids in nature is quite intense, with the abundance of species restricted by competition for limiting resources rather than other factors (i.e., weather or other density-independent factors). Johnson's presentation of the niche concept captures the essence of Grinnell's (1917) definition, by focusing on how overall resource availability limits a species' abundance and distribution. At the same time, by mentioning competition for resources, Johnson captures the essence of Elton's (1927) niche definition that focuses on species' impacts on their resources.

However, it is clear that Johnson himself was deeply skeptical of the niche worldview. He goes on to say:

> "*[However], the major species of the coccinellids do not seem to be so distributed. With certain exceptions…the species of* Hippodamia *and* Coccinella *are in quite general competition. They are characterized for the most part by very wide distribution and extensive overlapping of other species…The conclusion seems evident that the exigencies of the death-rate are great, and that these species have difficulty in leaving 2 progeny for each pair, not because of overcrowding, but from some other unfavorable circumstance…*[A species' density] *is not checked by any coccinellid saturation of the environment, and depends largely upon the degree of success it has in the distribution of its eggs and in its success in hibernation*." (Johnson 1910, pages 87-88)

Thus, Johnson felt that competition for resources was rare, and niche overlap broad, with coccinellid densities instead limited by harsh weather and other density-independent effects. So, Johnson was an early critic of the niche concept that he himself first presented.

Lady beetles clearly also influenced Elton's (1927) initial development of his "trophic niche" concept. Particularly influential on Elton was Richards' (1926) monograph on feeding relationships among English heath species: Elton mentions this study repeatedly in his discussion of the niche (Chapter 5; Elton, 1927). Richards (1926) notes in particular the rich abundance of insect life in *Pinus* groves on a British heath, and how so much of this insect life is supported by pine aphids (*Dilachnus pini* L.) and their predators, including coccinellids (Fig. 1). Richards made two important contributions to the development of trophic theory in coccinellid communities, and in communities more generally. First, he noted the great diversity of predators congregating at aphid infestations, and how these predators likely act together to limit aphid numbers. Second, he pointed out that spiders, in particular, often act as intraguild predators that feed both on herbivores and other predators competing with them for herbivorous prey:

> "*Spiders build their webs all over the pines and catch the winged individuals of the aphids, and also the adults of their* [the aphids'] *enemies*." (Richards 1926, Page 263)

In summary, lady beetles are the prototypical niche occupants, something that cocinellid enthusiasts can take pride in. Lady beetles also influenced early thinking on biodiversity-herbivore suppression relationships, and the role of intraguild predation. These initial studies of coccinellids helped to provide the framework for the creation of the niche concept, in the senses of both Grinnell's (1917) and Elton's (1927) perspectives. I next review studies of coccinellids' resource-requirement niches, and then those examining how coccinellids embedded within diverse communities impact their prey resources, later noting the general concordance in results collected from these two perspectives and how findings from one perspective can inform the other.

3. Impact of the environment on lady beetle diversity

Ecologists with a fondness for lady beetles have conducted a number of examinations of how the environment shapes lady beetle biodiversity. Differing food preferences among predator species is one obvious route to their occupying distinct niches (e.g., Finke and Snyder 2008). However, unlike many other predators, it was long believed that aphidophagous coccinellids, the best studied group of lady beetles, had little ability to follow chemical or other signals to track prey over long distances. Rather, it was believed that these lady beetles move through the environment repeatedly sampling habitats, with prey arresting further dispersal once physically contacted (Hagen, 1962; Hodek and Honěk, 1996). However, there is growing evidence that coccinellid foraging behavior may in fact be impacted by prey- or competitor-specific chemical cues, and such general indicators of prey activity as honeydew or plant volatiles (Hamilton et al., 1999; Zhu et al., 1999; Raymond et al., 2000; Jamal and Brown, 2001, Le Ru and Makosso, 2001; Ninkovic et al., 2001; Girling and Hassall, 2008; Khan et al., 2008; Seagraves, 2009, this issue). Particularly well-studied, although generally under laboratory conditions, is the tendency of many coccinellid species to use chemical cues to avoid ovipositing at sites where other conspecific or heterospecific predators have deposited their eggs (Kosaki and Yamaoka, 1996; Hemptinne et al., 2001; Seagraves, 2009, this issue). Similarly, aphid parasitoids and other competitors for aphids often avoid sites where coccinellids have recently foraged, apparently in response to chemical trails left by the coccinellids (Taylor et al., 1998; Nakashima and Senoo, 2003; Nakashima et al., 2004, 2006; Shiojiri and Takabayashi, 2005). Nonetheless, it may be that much “prey choice” by predaceous coccinellids occurs only as an indirect result of differing innate preferences for particular habitats, in either space or time. Of course, it is nonetheless clear that different coccinellid species differ in food requirements for growth and reproduction (Biddinger et al., 2009; Evans, 2009; Hodek and Honěk, 2009; Lundgren, 2009; Sutherland and Parrella, 2009; all this issue).

Resource-use differences have been documented to reflect responses of coccinellids to the habitat at scales ranging from individual plants to entire regional landscapes. Other studies have examined temporal (daily or seasonal) differences in activity-patterns among coccinellids and other co-occurring predator species, or have shown that coccinellids may differ from other predator species in their prey selection criteria.

3. 1. Spatial coccinellid niches. Particular attention has been focused on how predator species partition foraging space on plants. Plant traits such as cuticular wax density and leaf morphology affect predator foraging efficiency (Shah, 1982; Carter et al., 1984; Kareiva and Sahakian, 1990; White and Eigenbrode, 2000), and thus likely also affect the abilities of different predator species to utilize particular plant morphotypes or structures. For example, Schellhorn and Andow (1999) examined the implications of oviposition location for coccinellid species co-existence on corn (*Zea mays* L.). They found that one common coccinellid species, *Adalia bipunctata* L., preferred to forage and also oviposit high on corn plants where most aphids congregated. A second species, *Coleomegilla maculata* De Geer, preferred to forage and oviposit lower on plants, despite the fact that this kept them away from most aphid prey. These habitat-use differences made intraguild predation rare, but egg cannibalism relatively common. Schellhorn and Andow (1999) predicted that habitat partitioning among the two coccinellid species should lead to complementary impacts on aphids, and thus greater suppression by multi-species assemblages. This is a clear example of how research on habitat use suggests ways that predator species are likely to exert complementary impacts on their prey. Unfortunately though, this prediction was not experimentally tested. The tendency of *C. maculata* to forage lower on plants appears also to foster this species' coexistence with the invasive coccinellid *Harmonia* *axyridis* (Pallas) which, like *A. bipunctata*, prefers to forage near aphid infestations higher on plants (Musser and Shelton, 2003; Hoogendoorn and Heimpel, 2004).

A similar partitioning of plant space occurs in other systems. Nakashima and Akashi (2005) found that most predators aphids on alfalfa (*Medicago sativa* L.) in Japan congregate at the tops of plants, but that *Hippodamia tredecimpunctata* Say is evenly distributed across both the tops and bottoms of alfalfa stems. Thus, *H. tredecimpunctata* likely fills an important feeding niche as a predator of aphids lower on plants. Costamagna and Landis (2007) found that few predators foraged for soybean aphids (*Aphis glycines* Matsumura) lower on soybean (*Glycine max* L.) plants, providing a refuge for the aphid from predation. This may be an example of an open niche, such that addition to the system of a predator foraging at the base of soybean plants would strengthen overall herbivore suppression.

Several studies have considered habitat partitioning at a much larger scale, that of regional landscapes. For example, Honěk and Rejmánek (1982) collected over 20,000 coccinellids in central Bohemia in the Czech Republic, recording species co-occurrence and habitat associations. Using cluster analysis, they found distinct coccinellid communities in open, newly planted agricultural fields; shaded, more mature agricultural fields; and on weeds and trees. Particular species defied categorization by habitat, however. For example, *Coccinella septempunctata* L. occurred as a dominant species in all of these communities, whereas *A. bipunctata* was associated with high-density aphid colonies regardless of habitat type (Honěk and Rejmánek, 1982; Honěk, 1985). In a similar study in North American wheat fields, Elliott et al. (1998) found that coccinellid species responded to habitat heterogeneity at different scales, depending on their dispersal abilities. For example, the poor disperser *Coleomegilla maculata* was most common in landscapes that were patchy on the finest scale measured (within 1.7 km of sampled fields), whereas abundance of the widely dispersing coccinellid *Hippodamia convergens* Guérin-Méneville was positively correlated with patchiness (defined as the density of borders between different habitat types, with different habitats including grasslands, agricultural fields of various types, wetlands, and woodlots) at the scale of ca. 5 km. The location of overwintering sites can have a similar effect on coccinellid community structure, with particular species more likely to be found foraging in habitats close to the habitats they use for overwintering (Elliott et al., 2002).

3. 2. Temporal niches. On a fine temporal scale, Pfannenstiel and Yeargan (2002) observed predation of *Helicoverpa zea* (Boddie) eggs on corn over 24 hour periods. They found that *C. maculata*, the most abundant predator species, primarily foraged during the day. In contrast, *Nabis* sp., the second most abundant predator taxon, fed primarily at night. These temporal differences in predator activity seem to be widespread if not universal in agroecosystems (Weber et al., 2009), and would presumably reduce negative predator-predator interactions, heightening complementary impacts on prey.

However, most studies have examined temporal niches over much longer scales, that of entire cropping cycles. A particularly nice example was presented by Neuenschwander et al. (1975), who recorded the seasonal phenology of a diverse community of predators attacking aphids in California alfalfa fields. They concluded that most aphid predation was exerted by two *Hippodamia* species, with *H. convergens* active somewhat earlier in the year than *Hippodamia quinquesignata* (Kirby). However, other predator species also filled important seasonal gaps, with brown lacewings active before either coccinellid species, *Geocoris* and *Nabis* bugs active when aphid densities were low (and coccinellids inactive) during the hottest part of the summer, and syrphids and green lacewings causing mortality when aphids escaped control by coccinellids.

Thus, the authors concluded that only a diverse community of aphid predators could suppress aphids throughout the growing season (a pattern also discussed by Obrycki et al., 2009, this issue). A similar seasonal partitioning of the prey resource appears to occur among related predator species on alfalfa in Japan (Nakashima and Akashi, 2005).

Another example is provided by Hironori and Katsuhiro (1997), who found seasonal niche differences between *Coccinella septempunctata* and *Harmonia axyridis* attacking aphids on Japanese hibiscus trees. *Coccinella* arrived before, and *Harmonia* after, peak aphid outbreaks, suggesting temporal complementarity between the two species. However, *H. axyridis* was an aggressive intraguild predator of *C. septempunctata*, perhaps negating any benefit of these niche differences for aphid control. Similarly, Dixon et al. (2005) documented that predatory syrphids occur on British sycamore trees, and in wheat fields in the Czech Republic, during relatively cool weather early and late in the growing season. In contrast, coccinellids are most active during hot weather, suggesting seasonal niche differences that could lead to complementary impacts on shared prey. A meta-analysis of published developmental patterns for a wide variety of syrphid and coccinellid species suggested that seasonal niche differences may be common between these two taxa (Dixon et al., 2005). As a final example, minute pirate bugs (*Orius insidiosus* Say) feed heavily on soybean aphids (*Aphis glycines* Matsumura) in Midwestern U.S. soybean (*Glycines max* L.) fields early in the season, intercepting initial aphid colonists (Harwood et al., 2007). This likely slows early-season buildup of aphid populations, but only later-arriving coccinellid predators exert significant mortality later in the season as aphid densities grow too high to be substantially impacted by minute pirate bugs (Costamagna and Landis, 2007; Costamagna et al., 2007, 2008). In this way there may be seasonal complementarity in the impacts of *Orius* and the coccinellids, although this has yet to be tested.

3.3 Niche differences along both spatial and temporal axes. Smith (1971) examined spatiotemporal niche separation on the scale of 9 m^2 subplots within a field of corn in Ontario, Canada, over a growing season. Four coccinellid species were common, *Hippodamia tredecimpunctata tibialis* (Say), *Coccinella novemnotata* Herbst, *Coccinella transversoguttata richardsoni* Brown, and *Coleomegilla maculata lengi* Timberlake. Densities of *C. maculata* were relatively constant throughout the season, apparently reflecting this species' ability to utilize non-aphid prey, whereas the other three species clearly were most abundant roughly coincident with peak pollen and aphid availability. *Coleomegilla maculata* and *H. tredecimpunctata* tended to concentrate at the center, and *Coccinella novemnotata* and *C. transversoguttata* the perimeter, of the corn field. Thus, different species were distributed differently through both space and time, although the mechanistic bases of these differences were not clear. For example, differing distribution patterns could result from differences in colonization behavior, differences in movement through the environment after arrival, or both. Nonetheless, spatiotemporal separation among species should encourage greater coverage of the corn crop throughout the growing season, and thus complementary impacts on prey.

Similarly, Coderre et al. (1987) recorded egg-laying sites among a community of four aphid predators on corn plants in southern Quebec. Common predators were two coccinellids (*Coleomegilla m. lengi* and *Hippodamia tredecimpunctata tibialis*), a syrphid fly (*Sphaerophoria philanthus* Meigen), and a lacewing (*Chrysopa oculata* Say). All predators tended to deposit eggs on leaf undersides. However, there were clear spatial and temporal differences in oviposition behavior of the species. *Coleomegilla* generally laid eggs lower on plants that were away from field margins, and largely irrespective of proximity to aphids or overall aphid density.

In stark contrast, *Hippodamia* more often laid eggs on plants at field margins, near to large aphid colonies and concurrent with peak aphid abundance. The syrphid deposited eggs near the ground, like *Coleomegilla*, but generally only after aphids became abundant, while the lacewing laid its eggs late in the season and away from aphid colonies. Thus, there were clear differences in oviposition behavior among species when taking into account both spatial and temporal niche axes. Together, these data suggest that the co-occurrence of multiple predator species would even out the spatiotemporal distribution of attacks on aphids.

3.4 Prey choice niches. Dixon and Hemptinne (2001) found that coccinellid size distributions reflected those of their prey in a variety of world regions. This explanation fits closely with the verbal model of Elton (1927) that species' body sizes mirror the size distributions of their prey. Similarly, among aphidophagous coccinellids, smaller body size may allow coccinellids to thrive at relatively low aphid densities compared to larger coccinellid species (Honěk et al., 2008). This in turn can lead to temporal separation in activity, with smaller coccinellid species moving into aphid colonies relatively early in aphid-colony population growth, and larger coccinellid species arriving later (Honěk et al., 2008).

Two studies have examined another possibility, which is that coccinellids partition resources with other aphidophages based on innate color preferences (Seagraves, 2009, this issue). Lorenzetti et al. (1997) examined colonization of corn plants of different colors, with plants made more yellow through the withholding of nutrients (these plants were compared to fertilized, relatively green plants). They found that coccinellids tended to be more common on nutrient-starved yellow plants, whereas lacewings were more abundant on well-fed green plants. Of course, a wide variety of other characteristics correlated with plant color might truly underlie these differences in preference. Presumably, differences in host plant selection would lead to different predator species attacking different subsets of the prey population. Similarly, Losey et al. (1997) found that *Coccinella septempunctata* adults preferred to attack red color morphs of the pea aphid in Wisconsin, USA, alfalfa fields, whereas females of the parasitoid wasp *Aphidius ervi* Haliday preferentially attacked green color morphs of this aphid. Such differences in color preference would presumably lead to the coccinellid and parasitoid exerting complementary impacts on the pea aphid population as a whole.

3.5. Summary of research on resource-requirement niches. It appears to be common for different coccinellid species to respond differently to their environment, leading to species segregation in both space and time. Spatiotemporal differences in habitat use occur at the finest (single plants, single days) and broadest (whole regions, entire seasons) scales examined. Such spatiotemporal niche partitioning likely has several important implications: 1) intraspecific competition for prey should exceed interspecific competition, matching the preconditions for species co-existence proposed by MacArthur and Levins (1967); 2) overall prey consumption by multi-species predator communities should exceed that exerted by any single species (Finke and Snyder, 2008); and 3) intraguild predation should be uncommon because species rarely co-occur in precisely the same habitat at precisely the same time (Schmitz, 2007). For all of these reasons, we would expect diverse predator communities to exert the strongest herbivore suppression.

4. The impacts of diverse predator communities on prey.

A growing number of experimental studies examine the relationship between predator biodiversity and the strength of herbivore suppression, and this topic has been extensively reviewed (Duffy, 2002; Snyder et al., 2005; Ives et al., 2005; Tscharntke et al., 2005; Cardinale et al. 2006; Casula et al., 2006; Straub and Snyder, 2006a; Schmitz, 2007; Straub et al., 2008). In these studies, declining herbivore suppression at higher predator diversity levels is generally attributed to intraguild predation (Finke and Denno, 2004, 2005). A more complex group of mechanisms may underlie improving herbivore suppression with greater predator species richness (Snyder et al., 2005; Ives et al., 2005). Species identity or “sampling” effects occur when diverse communities perform relatively well because, by chance alone, such communities are more likely to include particularly effective species (e.g., particularly voracious predators). Most authors do not consider sampling effects to be “true” diversity effects, because sampling effects result from the attributes of particular, singular species, rather than any emergent property of diverse communities. However, opinions vary on this point (Walker, 1992; Rosenfeld, 2002; Chase and Leibold, 2003). Additivity occurs when predators neither heighten nor reduce prey capture by other species. Additivity can yield a positive relationship between diversity and herbivore suppression when overall predator abundance increases at higher diversity levels (e.g., Cardinale et al., 2003). Complementarity (= niche partitioning) occurs when species use different subsets of the resource pool (e.g., predators that attack different prey species or stages), and facilitation occurs when one predator indirectly increases prey capture by a second predator species (e.g., prey fleeing from one predator species fall victim to a second predator species). Complementarity and facilitation can yield super-additive diversity effects, wherein the impact of diverse communities exceeds what would be expected by a simple summation of the individual impacts of constituent species. In this case, the improvement in pest suppression at higher diversity levels is greater than what is achieved through simple additivity.

Some predator diversity studies use additive, and others substitutive, manipulations of predator diversity. Interpretation of these two designs differs (reviewed in detail by Straub and Snyder [2006a]). Additive designs hold intraspecific interactions constant by keeping densities of each predator constant across diversity levels, such that total predator density increases together with diversity (Straub and Snyder, 2006a). Thus, for additive designs, emergent effects of diversity are revealed when the combined impacts of multiple predator species exceeds the <u>sum</u> of their individual impacts (more or less; see Sih et al. [1998]). In contrast, substitutive designs hold total predator densities constant across diversity levels, in order to isolate impacts of predator species richness from those of predator density. This means that intraspecific interactions are increasingly relaxed at higher diversity levels (Connolly, 1988). In substitutive designs, emergent biodiversity effects are revealed when the combined impacts of multiple species exceeds the <u>average</u> of their individual impacts.

For coccinellids, a vast number of studies have examined interactions among species pairs, often in simple laboratory arenas. However, for the purposes of this review, I defined diversity studies as those examining <u>three or more</u> predator species, with multiple levels of species richness included as treatments (i.e., not just predators present versus absent), all species (or guilds) present as a component of the "low diversity" treatment, and at least one coccinellid species as a community member. The need to accommodate three or more predator species means that such experiments generally are often conducted in relatively large experimental arenas, including plants and often in the field. The studies I next review variously revealed super-additive, additive, and sub-additive multi-predator-species effects. However, positive (additive or super-additive) diversity effects were much more common than negative (sub-additive) ones. Many studies explicitly examined mechanisms underlying these diversity effects, a rarity in the biodiversity-ecosystem function literature as a whole but a clear strength of studies including coccinellids.

4.1. Super-additive predator diversity effects. In a truly visionary series of experiments, Tamaki and Weeks (1972) examined the effects of predator and prey diversity on the biological control of aphid and lepidopteran pests of sugarbeet (Table 1). The predator community included the coccinellid *C. transversoguttata* and the predatory bugs *Geocoris bullatus* (Say) and *Nabis americoferus* Carayon. In these experiments diversity was manipulated within a substitutive design, such that total predator abundance was constant across species richness levels. When either aphids or caterpillars were the sole prey, species identity effects dominated: *C. transversogutta* was the most effective at killing aphids, while *N. americoferus* was the most effective at killing caterpillars, such that greater diversity only acted to dilute the benefits of these most-effective single predator species. Surprisingly though, diverse predator communities outperformed the average across single predator species when both aphids and caterpillars were present. This super-additive interaction occurred because only diverse communities paired the aphid-killing potential of *Coccinella* with the caterpillar-killing potential of *Nabis*. Furthermore, by killing aphids the coccinellid removed these alternative prey from the community, allowing *Nabis* to focus its attacks on caterpillars (Tamaki and Weeks, 1972). Interestingly, Cardinale et al. (2003) report a similar result and mechanism, working in an alfalfa system (Table 1). In this case, the coccinellid *Harmonia axyridis* depressed densities of cowpea aphids (*Aphis craccivora* Koch) within diverse predator communities, allowing the parasitoid *Aphidius ervi* to concentrate its attacks on pea aphids. Thus, pea aphid control was effective only when all predator species occurred together. Because only pea aphids harmed plant growth, alfalfa yield also increased only when a diverse predator community was present. Thus, in both of these first two examples, it was the partitioning of prey species (to a degree) among different predators that led to their super-additive effects when combined.

Wilby et al. (2005) reported another example of niche partitioning among predator species, but in this case super-additive effects resulted from predators partitioning different prey life stages. They manipulated diversity among a community of generalist predators common in rice paddies in Vietnam, which included a lady beetle, a cricket, a plant bug, and a wolf spider. Two herbivorous prey species were considered, a planthopper with nymphal instars quite similar in form to one another, and a moth where the larval versus pupal stages were morphologically quite different (Table 1). Results differed for the two herbivore species. Mortality increased with greater predator biodiversity for the moth, but not the planthopper. This difference was attributed to life history differences, with the changing morphologies of the moth providing opportunities for different predator species to partition attacks among the different life stages. In contrast, all predators had similar impacts on the morphologically-similar planthopper stages, perhaps leading to ecological redundancy. However, prey stages may also differ in nutritional value to particular predator species and/or stages (Hodek and Honěk, 2009, this issue), such that other factors cannot be convincingly excluded without further experimentation. Also, it is not possible to draw general conclusions about differences from single examples of insects with simple versus complex development. Nonetheless, the results were consistent with theory by these same authors (Wilby and Thomas, 2002) suggesting that predators that partition their attacks among different herbivore life stages are particularly likely to complement one another, leading to super-additive impacts on prey.

Snyder et al. (2006) examined predator diversity effects among a community of predators and parasitoids attacking green peach and cabbage aphids on collards (Table 1). Included in the natural enemy community were the lady beetles *Hippodamia convergens* and *C. septempunctata*, an aphid-specialist parasitoid, and two species of predatory bug; predator diversity was manipulated within a substitutive design. Suppression of both aphids strengthened dramatically with greater predator biodiversity. For cabbage aphid, although not the green peach aphid, suppression by diverse predator communities significantly exceeded that exerted by the single best natural enemy species alone. This means that for cabbage aphid suppression, unambiguous super-additive diversity effects were certainly at work. Similar results were obtained when these experiments were repeated on both collard and potato plants, in different cages but in the same experiment and with green peach aphid as the sole prey species (Straub and Snyder, 2008).

In these collard and potato systems, super-additive effects of the predators appeared to result from spatial niche partitioning at the fine scale of individual leaves (Straub and Snyder, 2008). The coccinellids were the most voracious predators, but due to difficulty adhering to slippery surface waxes could forage only on stems and leaf edges. Bugs and parasitoids could access aphids anywhere on the plant. Thus, only diverse predator communities paired voracious coccinellids with predation on aphids in the spatial refuge from coccinellid predation (Straub and Snyder, 2008). Greater biodiversity also improved suppression of the green peach aphid on potato, although on that plant any spatial refuge from coccinellids was small, because leaves were smaller and less slippery, and thus the magnitude of the positive biodiversity effect was also much smaller (Straub and Snyder, 2008). Thus, it was partitioning of foraging space among species that underlay the super-additive effects that were observed in these diverse communities. This study demonstrates how partitioning of plant space among predator species, which we reviewed earlier (Section 3.1), can translate into significantly stronger herbivore suppression when predator communities are diverse. In contrast, unlike the studies by Tamaki and Weeks (1972) and Cardinale et al. (2003), in the collards system partitioning among aphid species appears to be unimportant in yielding super-additive multi-enemy effects (Snyder et. al, 2008).

The examples discussed so far all implicate niche partitioning, of one sort or another, as the mechanism leading to improved herbivore suppression with greater predator diversity. In addition, Losey and Denno (1998) provide clear evidence for predator-predator facilitation that leads to super-additive multi-predator effects. These authors found that *C. septempunctata* adults foraging in alfalfa foliage triggered dropping behavior by pea aphids, a common predator-escape behavior for this aphid species. Once on the ground the pea aphids were then subjected to predation by *Harpalus pensylvanicus* DeGeer ground beetles, which otherwise rarely encounter pea aphids. Thus, the impacts of coccinellid and ground beetle together exceeded the sum of the species' individual impacts, as in the absence of ground predators aphid apparently were able to safely return to their feeding positions on plants. For reasons that were never clearly explained, combined effects of *C. septempunctata* and a ground-dwelling rove beetle (*Philonthus* sp.) were not super-additive (Losey and Denno, 1998). Ground beetles sometimes aggregate near aphid outbreaks (Winder et al., 2005) despite the obvious spatial separation between aphids and ground beetles (but see Snyder and Ives, 2001), suggesting that such synergism between foliar and ground predators may be more common in nature than has been realized. Spatial-niche separation between predator species is a precondition for facilitation of this type, such that complementarity and facilitation cannot easily be disentangled from one another.

Ramirez and Snyder (in review) provide another example of super-additive effects due to facilitation. Here, the system was a community of predators (including the coccinellid

Hippodamia convergens) and pathogens attacking Colorado potato beetle (*Leptinotarsa decemlineata* Say; Coleoptera: Chrysomelidae) on potato plants (Table 1). Potato beetles are attacked by the predators while feeding in the foliage, and the pathogens once they move into the soil to pupate. This leads to the type of spatiotemporal separation among natural enemy species that has commonly been recorded within communities including coccinellids (reviewed in Sections 3.1-3.3). Consistently, the strongest herbivore suppression was exerted by diverse communities that included at least one predator and one pathogen species. This occurred because exposure to predators earlier in development rendered surviving potato beetle larvae more susceptible to pathogen infection. Apparently, the deployment of behavioral and chemical defenses to fend off predator attack came at a substantial physiological cost, leaving fewer resources to devote to immune function. Thus, rather than spatiotemporal niche partitioning being the driver of super-additive predator-pathogen effects, these natural enemies interacted by enforcing an internal tradeoff for the herbivore in resources devoted to anti-predator versus anti-pathogen defenses (Ramirez and Snyder, in review).

Aquilino et al. (2005) conducted a fully-factorial manipulation of predator and plant diversity, and measured resulting effects on pea aphid suppression. The three predator species were *Harmonia axyridis*, *Coleomegilla maculata*, and the predatory bug *Nabis* sp., and the three plant species were alfalfa, fava bean, and red clover (Table 1). The effects of diversity at the two trophic levels were opposing and of equal intensity (± 14% change in aphid suppression), with greater predator diversity leading on average to fewer aphids but plant diversity leading on average to more aphids. However, these effects were independent of one another, such that there was no interaction between predator and plant biodiversity. Diversity effects of both types appeared to reflect species identity (sampling) effects, rather than pure diversity effects.

Harmonia axyridis exerted stronger per capita aphid suppression than did either of the other two species, and inclusion of this single very effective species improved predator complex performance. Similarly, all species were relatively poor foragers on fava bean, and inclusion of this plant species lowered overall aphid suppression in plant polycultures.

4.2. Additive predator diversity effects. Evans (1991) compared predation of pea aphids by 3rd instars of *Hippodamia convergens* alone, versus *H. convergens* larvae paired with 3rd instars of other coccinellid species (either *Hippodamia tredecimpunctata*, *Hippodamia sinuata* Mulsant, or *Coccinella septempunctata*), on single fava bean (*Vicia faba* L.) plants. Surprisingly, even when *H. convergens* was paired with the superficially very different, and relatively distantly related, species *C. septempunctata*, there was no change in aphid consumption with increased biodiversity (one versus two species). Indeed, within the conditions of this experiment, any of the other species exerted effects entirely redundant with those of *H. convergens*. Flowers et al. (2006) found similar results working with three beetle predators of hemlock woolly adelgid on hemlock trees in the eastern United States. The predatory beetle guild included the coccinellids *Sasajiscymnus tsugae* Sasaji and McClure and *Harmonia axyridis*, and a predatory derodontid beetle (Table 1). Predator communities including one (at two densities), two or all three species were constructed using sleeve cages on hemlock trees in the field, to measure resulting impacts on predator reproduction and adelgid predation. Intraspecific predator interference was clearly important, with per capita reproduction and impacts on prey declining for all species when moving from one to two individuals. However, there was little interspecific interaction, with multi-species pairings exhibiting apparently additive impacts on prey, although statistical tests of this were not performed. Thus, in both cases, increasing the number of predator species was observed to, (Flowers et al., 2006) or would be expected to (Evans, 1991), strengthen herbivore suppression with greater diversity, assuming a positive relationship between predator diversity and overall predator abundance.

Schmidt et al. (2003) and Snyder and Ives (2003) examined the individual and combined effects of two guilds of aphid natural enemies, parasitoids and generalist predators, and found remarkably similar results. Schmidt et al. (2003) worked with the community of natural enemies attacking grain aphids on cereal crops in Europe, which is composed of a speciose group of parasitoid wasps, spiders, and ground beetles (Table 1). Coccinellids were present but relatively rare. Predators were manipulated to establish a 2 × 2 factorial manipulation of foliar natural enemies (present or absent) crossed with ground predators (present or absent). The authors found that the impacts of foliar and ground predators were almost perfectly additive, with no evidence of either disruptive or super-additive effects, such that aphid suppression was greatest with both natural enemy guilds present. Snyder and Ives (2003) conducted nearly identical experiments, but working with the community of pea aphid predators (primarily ground beetles, predatory bugs, and coccinellids) and the parasitoid *A. ervi*, on alfalfa in North America. These authors also found that the impacts of these two natural enemy guilds were almost perfectly additive. The generalist predator guild exerted relatively constant, apparently density-independent mortality throughout aphid population growth, whereas parasitoids acted in a density-dependent manner to strongly suppress peak aphid densities at the height of aphid population growth. Thus, in this sense predators and parasitoids were complementary to one another.

4.3. Sub-additive predator diversity effects. Rosenheim et al. (2004) examined the impacts of a diverse predator community on carmine spider mite herbivores of papaya (Table 1). Mite-specialist predators in the community included the coccinellid *Stethorus siphonulus* Kapur and a staphylinid beetle, along with a generalist tangle-web spider (Table 1). The specialists foraged widely in search of their sedentary prey, and this subjected them to intraguild predation by the sit-and-wait spider. Indeed, when all three predator species were present together, the tangle-web spider preyed heavily upon *Stethorus*, and this intraguild predation disrupted herbivore suppression. Finke and Denno (2005) reported quite similar interactions within a similarly structured community of predators attacking planthoppers on salt marsh cordgrass (Table 1). The predator community included three strict predators (the lady beetle *Naemia seriata* Melsheimer, a mirid bug and a web-building spider) that fed only on planthoppers, and two hunting spider intraguild predators, that ate both planthoppers and the strict predators (although, not *N. seriata*) (Table 1). Drawing from this pool of predator species and within an additive design, these authors created predator communities including one, two or three predator species. When communities included only strict predators, the species had additive effects such that total herbivore suppression, and resulting plant protection, grew with greater diversity. However, effects of intraguild predator species were sub-additive, weakening herbivore suppression and plant protection with greater predator diversity. Costamagna et al. (2007) report a similar example of disruptive intraguild predation, although here the magnitude of disruption was small. These authors separately manipulated a guild of generalist predators (primarily the lady beetle *H. axyridis*, but also minute pirate bugs, a predatory gall midge, and a lacewing) and a parasitoid wasp (Table 1) attacking soybean aphid on soybean. Activity of the parasitoid was disrupted in the presence of the predators, apparently through some combination of intraguild predation and exploitative competition for prey. The difficulty in distinguishing between intraguild predation of parasitoids leading to lower parasitoid densities in subsequent generations, versus competition for prey leading to the same effect, is common to many studies of predator-parasitoid interactions (discussed in Colfer and Rosenheim, 2001). Fortunately, interference through either mechanism seems to yield similar effects on resulting aphid densities (Rosenheim and Harmon, 2006). Regardless, in the soybean system, because *H. axyridis* had a dramatically stronger impact than any other enemy species, aphid suppression was similarly strong whenever that species was present (see also Gardiner and Landis, 2007; Costamagna et al., 2008).

Cardinale et al. (2006) manipulated predator diversity (one versus three species), among an assemblage of coccinellids that commonly attack pea aphids in alfalfa (Table 1), and found that combined aphid suppression by all three species was less than would be predicted based on their individual performances alone. The authors suggest that the presence of *C. septempunctata* drove the other two coccinellid species to suboptimal foraging locations on plants, reducing the net foraging efficiency of the guild as a whole. It is unclear precisely how this displacement worked, although intraguild predation was not observed so perhaps avoidance was chemically-mediated (e.g., Seagraves, 2009, this issue). Whatever the specific mechanism, in this case predator-predator interference occurred in the absence of intraguild predation.

4.4. Summary of research on resource-exploitation niches. The literature contains multiple examples of super-additive, additive, and sub-additive effects of predator diversity on herbivore suppression. However, predator diversity effects that strengthened herbivore suppression (through either super-additive or additive multi-enemy effects) far outnumber negative effects (13 examples to 4; Table 1). In only two studies (Rosenheim et al. [2004] and Finke and Denno [2005]) did intraguild predation clearly lead to strong disruption of herbivore suppression at higher diversity levels. These two cases are similar to other examples of highly disruptive intraguild predation elsewhere in the literature, in their combination of highly effective specialist predators of the herbivore with generalists that are highly efficient intraguild predators (Ives et al., 2005). In another case that we found in the literature, intraguild predation was apparently too weak to yield a strongly negative relationship between biodiversity and biocontrol (Costamagna et al., 2007), while in an additional case of disruption intraguild predation did not occur (Cardinale et al., 2006).

Often, the performance of diverse communities clearly exceeded what would be expected based on the performance of constituent species when alone. These emergent, super-additive diversity effects were traced back to several different mechanisms. In most cases, niche partitioning was implicated as the underlying mechanism, with different predator species partitioning their attacks among different prey species (Tamaki and Weeks, 1972; Cardinale et al., 2003) or different life stages of a single prey species (Wilby et al., 2005), or partitioning their foraging among different parts of host plants (Straub and Snyder, 2008). Predator-predator facilitation has received a great deal of attention in the predator-prey literature (Sih et al., 1998), and interspecific facilitation appears to underlie many of the best-studied examples of improving resource consumption with greater diversity in non-predator systems (Hooper et al., 2005). Nonetheless, only the studies by Losey and Denno (1998) and Ramirez and Snyder (in review) found multi-enemy-species facilitation that clearly led to super-additive effects. Rarely did sampling effects explain the improved performance of diverse predator communities. However, in many cases coccinellids were among the most voracious/effective predator species in their communities (i.e., Tamaki and Weeks, 1972; Cardinale et al., 2003; Rosenheim et al., 2004; Snyder et al., 2006; Costamagna et al., 2007). This may be an important functional role of coccinellids, with these beetles providing uniquely gluttonous consumption of prey compared to the predator species in other taxa.

5. Trophic niches and coccinellid species displacement

Two species of coccinellid, *C. septempunctata* (native to Europe and Asia) and *H. axyridis* (native to Asia), have been particularly successful invaders in North America, often to the detriment of native coccinellids. Three scenarios might explain the ability of *C. septempunctata* and *H. axyridis* to invade and then dominate North American coccinellid communities. The first is that the invasive species would occupy previously vacant niches, consuming aphids that otherwise would not be subject to attack by native coccinellid species. Were this the case, total aphid densities would be expected to diminish as the invaders consumed previously unutilized prey, native species would be unaffected as there would be little resource overlap with the invaders, and overall coccinellid densities within a landscape or region would increase as the effective total resource pool increased (Table 2). The second possibility is that the invaders would competitively displace native species, taking over feeding niches previously occupied by natives. In this case, overall prey densities would decrease as the invaders deplete resources to levels too low to be utilized by the natives, densities of natives would decline as they were outcompeted, and overall coccinellid densities would be relatively constant as one species replaced another (Table 2). The final possibility is that coccinellids would displace native species through intraguild predation, following the mantra “why compete when you can eat”. In this case prey densities might increase as intraguild predation disrupted top-down control, native species would decline as they were eaten, and total coccinellid densities might decline reflecting the consumption of natives by invasives (Table 2).

The data accumulated to date suggest that the second of these scenarios, competitive exclusion of natives by exotics, is occurring. Harmon et al. (2007) uncovered seven long-term datasets that record information on coccinellid communities both pre- and post invasion by *C. septempunctata*, *H. axyridis*, or both species. Both studies (Alyokhin and Sewell [2004] and Evans [2004]) that recorded prey density over the complete time series found that aphid densities significantly declined following invasion. Across all studies there was no clear trend for significant change in the overall densities of native coccinellid species. However, it was clear that particular species, most significantly *C. septempunctata*'s native congeners *C. transversoguttata* and *C. novemnotata*, have become quite rare following invasion. Overall coccinellid densities appear to be unchanged pre- versus post- invasion. These patterns bear the hallmark of competitive displacement as the mechanism driving successful invasion (Table 2), but are not consistent with intraguild predation as the underlying mechanism. This provides evidence, albeit circumstantial, that resource-use differences among native species are contributing to their coexistence, and that this balance is disrupted following invasion of species with resource-use patterns similar to native species (for a time, until these natives are fully displaced and a new balance is achieved).

The clearest support for a role of competitive displacement in allowing the establishment of exotic coccinellids comes from the elegant series of experiments reported by Evans (2004). This work was conducted in Utah alfalfa fields, with pea aphid as the primary prey. Prior to 1994, coccinellid communities in these fields were dominated by *C. transversoguttata* and several *Hippodamia* species, all native. *Coccinella septempunctata* first arrived in Utah in 1993, and dominated the coccinellid communities by 1997. Concurrent with this invasion, native species became significantly less common in alfalfa, and pea aphid densities also significantly declined.

Evans hypothesized that competitive exclusion was driving natives out of alfalfa, as *C. septempunctata* drove pea aphids to densities too low to support foraging by the native species. As a test of this hypothesis Evans restored pea aphids to pre-invasion densities using protective cages, and then removed the cages to allow colonization by coccinellids. Pre-invasion prey densities drew natives back into these alfalfa plots; apparently, the natives had been displaced from alfalfa fields but remained in refuges elsewhere in the landscape. This experimental result provides unambiguous evidence that competitive exclusion was operating, at least in the case of *C. septempunctata*'s replacement of native coccinellids in Utah alfalfa fields.

6. Synthesis

Studies of niche relationships within coccinellid communities have been focused on ways that species respond to resources in the environment, and on the different ways that particular species impact their resources. From both perspectives, there is overwhelming evidence that coccinellid species generally differ from one another, and from other predator species, in ecologically meaningful ways. However, there are clear differences in the scales at which resource-requirement and resource-exploitation niches have been studied. Researchers interested in the impact of the environment on resulting coccinellid diversity sometimes undertake studies at the scales of single plants or over the course of single days, but most often significant niche differences are revealed at the scale of whole fields or regions, over the course of entire growing seasons. Due to logistical constraints, experimental studies of biodiversity-biocontrol relationships always consider smaller spatiotemporal scales, encompassing one or several plants and continuing over days or weeks. The caging that is necessary to manipulate species number also eliminates the field- and landscape-scale movement of coccinellids so important in yielding habitat-niche differences at larger scales. The fact that these experimental efforts so often find super-additive multi-predator effects, despite scales too small to reproduce many important niche differences, allows the possibility, yet untested, that positive diversity effects may be even more prevalent in nature than the experimental work has yet been able to capture. Only experiments at larger scales and/or in open plots will resolve this issue, although the logistical challenges to performing such a study with highly mobile predators are daunting.

As a whole, observational and experimental studies have revealed a large array of mechanisms leading to complementarity among coccinellid species, and between coccinellids and other predator species. For example, at the scale of landscapes, coccinellids segregate based on the scale at which their differing dispersal abilities allow them to take advantage of landscape-heterogeneity (Elliott et al., 1998). At the scale of fields, these predators appear to respond to their differing prey needs, while also perhaps minimizing the risk of intraguild predation (e.g., Coderre et al., 1987). At the scale of individual leaves, predators exhibit differing abilities to adhere to plants and thus to access aphid prey (Straub and Snyder, 2008). Similarly, differing thermal or other ambient-condition (e.g., humidity, light intensity, etc.) requirements can similarly lead to seasonal, and perhaps also daily, niche partitioning (Pfannenstiel and Yeargan, 2002; Dixon et al., 2005). Coccinellids also partition prey life stages (Wilby et al., 2005), or differ with other species in the prey species they are most effective at attacking (Tamaki and Weeks, 1972; Cardinale et al., 2003). All of these differences would be expected to increase the likelihood of positive multi-enemy effects that strengthen herbivore suppression (Ives et al., 2005), and indeed this is the most common result emerging from the experimental studies reviewed here (Table 1). Importantly, predator species that tend not to co-occur in space and time also will have few opportunities to engage in intraguild predation (Musser and Shelton, 2003; Schmitz, 2007), further tipping the balance toward positive diversity effects.

Perhaps the best evidence that these niche differences foster co-existence comes from the ecological effects of invasion by *C. septempunctata* and *H. axyridis*. These species depress prey densities and displace ecologically-similar native species, suggesting that species with similar niche requirements cannot coexist. This can be seen for example among the community of coccinellids on corn. *Coleomegilla maculata* forages on different locations on corn plants than does *H. axyridis*, and utilizes a broad range of non-aphid foods which also allows for niche segregation (Musser and Shelton, 2003; Lundgren et al., 2004). Perhaps it is no coincidence then that *C. maculata* appears relatively unaffected by the arrival of *H. axyridis*. In contrast, *Adalia bipunctata* and *H. axyridis* forage in similar locations and exploit the same high-density aphid colonies (Honěk, 1985; Schellhorn and Andow, 1999; Musser and Shelton, 2003); *A. bipunctata* populations decline following *H. axyridis* invasion. *Adalia bipunctata* failed to invade areas in Japan where *H. axyridis* is native, which would again be consistent with interference between these two coccinellid species (Snyder and Evans, 2006).

Intraguild predation has garnered a great deal of interest among predator ecologists in recent years. It has been proposed that strong intraguild predation could disrupt trophic cascades, perhaps even leading to increasing herbivore damage with increasing predator biodiversity (Finke and Denno, 2004). Similarly, studies of intraguild predation have dominated the recent coccinellid ecology literature (Lucas, 2005; Hodek and Michaud, 2008; Pell et al., 2008; Soares et al., 2008; Weber and Lundgren, 2009, this issue). It now is clear that many coccinellids are capable of engaging in intraguild predation, and that these interactions occur and can be important in the field (Hironori and Katsuhiro, 1997; Colfer and Rosenheim, 2001; Michaud, 2002; Snyder and Ives, 2003; Costamagna et al., 2007, 2008). However, there is growing evidence that intraguild predation rarely is sufficiently intense to entirely erase the top-down benefits of greater predator biodiversity. For example, Rosenheim and Harmon (2006) recently reviewed intraguild predation among insect predators, of necessity including mostly older studies that pair just two predator species together. Nonetheless, the conclusions were the same as were reached here when considering only manipulations of three or more predator species, which is that disruptive intraguild predation is rare and when it occurs, it generally has a weak effect on biocontrol. This is consistent with the observation that top-down trophic cascades are generally strong in nature, across a broad range of community types (Hawkins et al., 1999; Schmitz et al., 2000; Halaj and Wise, 2001), and suggests a relatively weak role for intraguild predation more generally.

While much progress has been made in recent years, this literature review reveals several unanswered questions that may serve as foci for future research:

1. Can we develop the capability to predict when predator diversity effects will be positive or negative? Recent studies have begun to reveal, after the fact, specific mechanisms leading to predator diversity effects. However, a predictive capability has remained elusive. The relatively small number of studies wherein predator diversity has been experimentally manipulated provides few good leads on community traits common to studies revealing diversity effects of one type or another. For example, lady beetle eggs and larvae are relatively susceptible to intraguild predation, and so negative diversity effects might be expected to be more likely in this case. However, studies including coccinellid larvae have revealed super-additive (Snyder et al., 2006), additive (Evans, 1991) and sub-additive (Rosenheim et al., 2004) predators diversity effects: all possible

outcomes are represented. Similarly, greater prey diversity sometimes leads to super-additive diversity effects (Tamaki and Weeks, 1972), as would be expected by providing greater opportunity for prey partitioning. However, this is not always the case (Snyder et al., 2008). Indeed, the inability to identify community trait distributions predictive of complementarity or other positive diversity effects remains a major challenge in biological control (Myers et al., 1989; Denoth et al., 2002) and ecology more generally (Petchey and Gaston, 2006).

2. How common is predator-predator facilitation in coccinellid communities? In the plant and detritivore communities that have received the most attention, facilitation appears to be the dominant mechanism leading to super-additive diversity effects (Hooper et al., 2005). Indeed, among predator communities many examples of facilitation among predator species pairs have been recorded (Sih et al., 1998), and the classic example of predator-predator facilitation involves the lady beetle *Coccinella septempunctata* (Losey and Denno, 1998). Why then does facilitation play such a modest role in coccinellid diversity studies to date? One possibility is that experimental studies encompass too narrow of a range of natural enemy species. For example, the inclusion of pathogens within a natural enemy community revealed facilitation that was not apparent if only predator species were considered (Ramirez and Snyder, in review).
3. Can we bridge the spatiotemporal gap between the scales at which resource partitioning is often recorded to occur (landscapes and seasons) with the scale at which predator diversity manipulations can be conducted? Due to clear logistical constraints predator diversity cannot be manipulated over entire landscapes over multiple years. But clever alternatives can be explored, for example combining correlations of landscape-scale

patterns of predator diversity with risk to their prey (e.g., Tylianakis et al. 2006, 2007) with smaller-scale manipulative experiments that reveal underlying mechanisms in the same system (e.g., those described in Table 1), may be a way to bring together pattern and process in predator diversity studies.

Conservation biocontrol schemes often encourage greater natural enemy biodiversity (Straub et al., 2008; Lundgren, 2009), as do organic agriculture and other environmentally-friendly approaches to farming (Bengtsson et al., 2005; Hole et al., 2005). Nonetheless, the relationship between biodiversity and biocontrol has, until recently, remained untested. The literature reviewed here suggests that the inclusion of coccinellid species in diverse predator communities, as a general rule, is likely to improve the efficiency of biological control. Predator biodiversity encourages more complete distribution of attacks on herbivorous pests in both space and time, as different coccinellid species pursue their inherent predispositions to occupy particular habitats and/or attack particular prey species or stages. Indeed, in several of the experimental case studies conducted so far, diverse predator assemblages including coccinellids exerted herbivore suppression exceeding that of even the most effective single predator species at high density (Table 1). In summary, the fear of intraguild predation that has gripped applied ecologists in recent years appears generally unwarranted, at least for communities including coccinellids as prominent members. Instead, with coccinellids as with many other aspects of life, it may be best to embrace diversity. The best niche fit for coccinellids may be as ecologically-unique predators that complement the impacts of other species, rather than that of disruptive intraguild predators.

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[Table 1 is attached]

Table 2. Three different mechanisms that might have fostered the invasion of North America by *Coccinella septempunctata* and *Harmonia axyridis*, the predicted ecological effects if each of these mechanisms the dominant force underlying invasion, and observed patterns from the seven pre- and post-invasion datasets reported by Harmon et al. (2007).

	Ecological effect		
Mechanism of invasion	Prey abundance	Abundance of native coccinellids	Total abundance of coccinellids
Vacant niche	Decrease	No change	Increase
Competitive displacement	Decrease	Decrease	No change
Intraguild predation	Increase	Decrease	Decrease
Observed	Decrease	Decrease	No change

Figure Legend

Fig. 1. Web of interactions among arthropods on a British heath, all anchored by pine aphids as the basal resource species. Arrows indicate the direction of energy flow. Many predator species contribute to suppression of pine aphids, although spiders also feed on other predators. Interactions re-drawn from Richards (1926).

Fig. 1

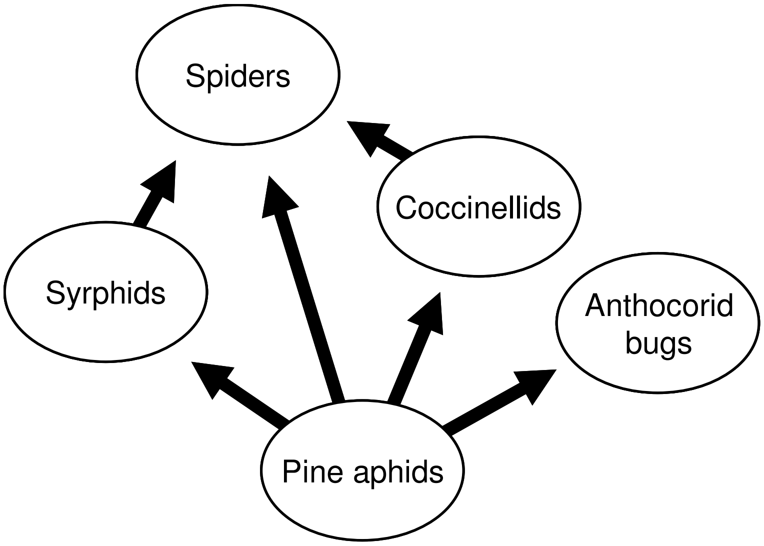

Table 1. Summary of studies in communities including at least one coccinellid species, where predator diversity was manipulated to measure its effects on herbivore suppression. See text for criteria for inclusion of studies.

Reference	Coccinellid species	Other predator species	Prey species	Plant species	Scale	Diversity Treatment	Design	Suggested Mechanism
Super-additive diversity effects (9)								
Tamaki and Weeks (1972)	*C. transversoguttata*	*Nabis americoferus*, *Geocoris bullatus*	Aphid (*Myzus persicae*) and 2 caterpillars (*Ceramica picta*, *Mamestra configurata*)	Sugarbeet (*Beta vulgaris*)	Greenhouse 9-13 days	0, 1, 2, 3 species	Substi-tutive	Partitioning of prey species
Cardinale et al. (2003)	*H. axyridis*	*Nabis* sp., *Aphidius ervi* (parasitoid)	Two aphids (pea aphid, *Acyrthosiphon pisum*, and cowpea aphid, *Aphis craccivora*)	Alfalfa (*Medicago sativa*)	Greenhouse 31 days	0, 1, 3 species	Add-itive	Partitioning of prey species
Aquilino et al. (2005)	*H. axyridis* and *C. maculata*	*Nabis* sp.	Pea aphid	Alfalfa, fava bean (*Vicia faba*) and/or red clover (*Trifolium pratense*)	Greenhouse 30 h	0, 1, 3 species	Substi-tutive	Sampling effect
Wilby et al.	*Micraspis crocea*	Cricket (*Metioche*	Brown planthopper	Rice (*Oryza*	Greenhouse	0, 1, 3	Substi-	Partitioning of

(2005)		*vittaticollis*), plant bug (*Cyrtorhinus lividipennis*), wolf spider (*Pardosa pseudoannulata*)	(*Nilaparvata lugens*) and rice leaf-folder moth (*Marasmia patnalis*)	*sativa*)	24 h	species	tutive	prey stages
Snyder et al. (2006)	*C. septempunctata* and *H. convergens*	Bugs (*Geocoris pallens* and *Nabis alternatus*), parasitoid (*Diaeretiella rapae*)	Green peach and cabbage (*Brevicoryne brassicae*) aphids	Collards (*Brassica oleracea*)	Field cages, 28 days	0, 1, 4 species	Substi-tutive	Habitat partitioning
Snyder and Straub (2008)	*C. septempunctata* and *H. convergens*	Bug (*N. alternatus*) and parasitoid (*Aphidius matricariae*)	Green peach aphid	Collards or potato (*Solanum tuberosum*)	Field cages, 14 days	0, 1, 4 species	Substi-tutive	Habitat partitioning
Snyder et al. (2008)	*C. septempunctata* and *H. convergens*	Bug (*N. alternatus*) and parasitoid (*D. rapae*)	Green peach and/or cabbage aphids	Collards	Field cages, 28 days	0, 1, 4 species	Substi-tutive	Habitat partitioning
Losey and Denno (1998)	*Coccinella septempunctata*	Ground beetle (*Harpalus pensylvanicus*) and	Pea aphid	Alfalfa	Field cages, 7 days	0, 1, 2 species	Add-itive	Facilitation

		rove beetle (*Philonthus* sp.)						
Ramirez and Snyder (in press)	*Hippodamia convergens*	Predators (damsel bug, *Nabis alternatus* and ground beetle, *Pterostichus melanarius*) and Pathogens (fungus, *Beauveria bassiana* and entomopathogenic nematodes, *Steinernema carpocapsae* and *Heterorhabditis marelatus*)	Colorado potato beetle, *Leptinotarsa decemlineata*	Potato	Field cages, 28 days	0, 1, 2, 5 species	Substitutive	Facilitation
<u>Additive diversity effects (4)</u>								
Evans (1991)	*H. convergens*, *H. tredecimpunctata*, *H.*	--	Pea aphid	Fava bean	Greenhouse 2 days	0, 1, 2 species	Substitutive	--

	sinuata, *C. septempunctata*							
Schmidt et al. (2003)	Not specified	A diverse group of spiders, ground beetles, parasitoid wasps	Grain aphid (*Sitobion avenae*)	Wheat (*Triticum* sp.)	Field cages, 3 weeks	0, 1, or 2 guilds (ground versus aerial)	Additive	--
Snyder and Ives (2003)	*C. septempunctata* and *H. axyridis*	*Nabis* sp. the ground beetle *Pterostichus melanarius*, the parasitoid *A. ervi*	Pea aphid	Alfalfa	Field cages, 21 days	0, 1, or 2 guilds (ground versus aerial)	Additive	--
Flowers et al. (2006)	*Sasajiscymnus tsugae*, *H. axyridis*	Derodontid beetle, *Laricobius nigrinus*	Hemlock woolly adelgid (*Adelges tsugae*)	Eastern hemlock (*Tsuga canadensis*)	Field sleeve cages, 4-6 weeks	0, 1, 2, 3 species	Additive	--
Sub-additive diversity effects (4)								
Rosenheim et al. (2004)	*Stethorus siphonulus*	Rove beetle (*Oligota sp.*), tangle-web spider (*Nesticodes*	Carmine spider mite (*Tetranychus cinnabarinus*)	Papaya (*Carica papaya*)	Open field, 10 days	0, 1, 2, 3 species	Additive	Intraguild predation

		rufipes)						
Finke and Denno (2005)	*Naemia seriata*	Mirid (*Tytthus vagus*), web spider (*Grammonota trivittata*), hunting spiders (*Pardosa littoralis*, *Clubiona saltitans*)	Planthopper (*Prokelisia dolus*)	Salt marsh cordgrass (*Spartina alterniflora*)	Greenhouse 2 months	0, 1, 2, 3 species	Additive	Intraguild predation
Cardinale et al. (2006a)	*H. axyridis*, *C. septempunctata*, *C. maculata*	--	Pea aphid	Alfalfa	Field cages, 18 days	0, 1, 3 species	Additive	Habitat displacement
Costamagna et al. (2007)	Primarily *H. axyridis*	Minute pirate bug (*Orius insidiosus*), gall midge (*Aphidoletes aphidomyza*), lacewing (*Chrysoperla carnea*), parasitoid (*Lysiphlebus*	Soybean aphid (*Aphis glycines*)	Soybean (*Glycine max*)	Field cages, 6 weeks	0, 1 or 2 guilds (parasitoid versus predator guild)	Additive	Intraguild predation

testaceipes)
