

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/223922997>

Influence of relative abundance and taxonomic identity on the effectiveness of generalist predators as biological control agents

Article in *Biological Control* · February 2010

DOI: 10.1016/j.biocontrol.2009.09.004

CITATIONS

9

READS

139

3 authors:



[Carlo R. Moreno](#)

University of California, Santa Cruz

2 PUBLICATIONS 179 CITATIONS

[SEE PROFILE](#)



[Scott Lewins](#)

University of Vermont

8 PUBLICATIONS 37 CITATIONS

[SEE PROFILE](#)



[Pedro Barbosa](#)

University of Maryland, College Park

35 PUBLICATIONS 1,089 CITATIONS

[SEE PROFILE](#)



Influence of relative abundance and taxonomic identity on the effectiveness of generalist predators as biological control agents

Carlo R. Moreno^{*}, Scott A. Lewins¹, Pedro Barbosa

Department of Entomology, University of Maryland, College Park, MD 20742, USA

ARTICLE INFO

Article history:

Received 8 March 2009

Accepted 8 September 2009

Available online 12 September 2009

Keywords:

Conservation biological control

Generalist predators

Natural enemy assemblages

Relative abundance

Additive effects

Intraguild predation

Pieris rapae

Coleomegilla maculata

Coccinella septempunctata

Podisus maculiventris

ABSTRACT

A central yet relatively untested assumption of conservation biological control is that an assemblage of naturally occurring natural enemies is more effective at controlling pests than any individual species within the assemblage. However, often ignored in this assumption is that natural enemies typically vary in relative abundance, such that one or a few species are highly abundant while most are relatively scarce. Little is known of the combined roles of relative abundance and taxonomic identity in the mortality imposed by assemblages of natural enemies on pest species. We investigated the influence of relative abundance and taxonomic identity among three generalist arthropod predators found in collards (*Brassica oleracea* var. *acephala*) on the mortality of the imported cabbageworm, *Pieris rapae*. We altered the relative abundance of the generalist predators in experimental mesocosms and determined the mortality of 1st instar cabbageworms. The impact of relative abundance on cabbageworm mortality was mediated by the taxonomic identity of the highly abundant predator. Further, the level of mortality imposed by highly abundant predators was in some cases influenced by the occurrence of intraguild predation involving less abundant predators. Our results suggest that the success of management strategies involving the preservation of highly abundant predators in managed systems via conservation biological control tactics may be dependent on the identity of both the highly abundant and scarce natural enemies.

© 2009 Elsevier Inc. All rights reserved.

1. Introduction

With several studies reaffirming the effectiveness of generalist arthropod predators as biological control agents (Settle et al., 1996; Holland et al., 1996; Chang and Kareiva, 1999; Symondson et al., 2002), the role of naturally occurring assemblages of generalist predators in suppressing pest populations has recently gained more attention. The putative importance of predator assemblages is particularly prominent in conservation biological control, where the central objective is to enhance pest mortality by preserving natural enemy communities present in managed habitats, primarily through cultural, agronomic, and ecological practices and manipulations (see Barbosa, 1998). While it has been shown that multiple predators can reduce pest populations more effectively than single species (Cardinale et al., 2003, 2006; Straub and Snyder, 2006; Snyder et al., 2006, 2008), there also is growing evidence that negative interactions such as intraguild predation and mutual interference can significantly dampen multi-enemy impacts rela-

tive to single, effective predator species (Rosenheim et al., 1993; Finke and Denno, 2004, 2005). Currently, there is increasing interest in identifying the “right” kind of natural enemy diversity needed to promote positive, pest suppressing interactions. However, despite numerous advances in identifying mechanisms by which natural enemy diversity enhances herbivore suppression as well as predator traits that directly or indirectly influence multitrophic interactions (Schmitz, 2007; Straub et al., 2008; Straub and Snyder, 2008; Letourneau et al., 2009), little has been done to clarify the role of relative abundance among multiple predators in regards to the mortality they collectively impose on pests.

Communities or assemblages of both plants and animals are generally characterized as having only one or a few species that are relatively abundant (i.e., numerically dominant), whereas the majority of the members of the assemblage are relatively scarce (i.e., numerically subdominant) with many of them occurring as singletons (Sugihara, 1980; Paarmann et al., 2001; Barbosa et al., 2005; McGill et al., 2007). The significance of sampling intensity as well as both stochastic (e.g., dispersal, local extinction) and deterministic (e.g., interspecific competition and other biotic interactions) factors in structuring communities and species abundance patterns has been the subject of many papers (Novotny and Basset, 2000; Ulrich, 2005; de Bello et al., 2007; Coddington et al., 2009). Nevertheless, many of the studies that have evaluated the impacts

^{*} Corresponding author. Present address: Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA. Fax: +1 831 4594015.

E-mail address: crmoreno@ucsc.edu (C.R. Moreno).

¹ Present address: Department of Plant and Soil Sciences, University of Vermont, Burlington, VT 05405, USA.

of natural enemy diversity on pest suppression have focused or utilized assemblages comprised of species of equal abundance (Cardinale et al., 2003; Finke and Snyder, 2008; Straub and Snyder, 2008). Furthermore, while the importance of relative abundance in assemblages and communities has been theoretically and empirically explored in many unmanaged habitats (see McGill et al., 2007 and references therein), the consequences of the pattern of relative abundance to the nature and outcome of interactions among predators in assemblages in managed habitats (and thus to the mortality imposed on pests) are still unclear.

Given that the interplay of positive and negative interactions in generalist predator assemblages can be a significant determinant of predator assemblage effectiveness (Snyder and Ives, 2001; Prasad and Snyder, 2004; Finke and Denno, 2004), it is important to determine how numerically dominant and subdominant predator species interact and collectively impact prey populations. Interactions among predators may be additive, whereby the total impact of an assemblage would be equal to the summed impacts of each species in the assemblage (Snyder and Ives, 2003). Alternatively, the impact of an assemblage may be positively non-additive; i.e., the combined mortality imposed on prey by all predator species is greater than the summed impact of each individual species. The enhanced impact is generally attributed to complementary resource use among predators (Soluk and Collins, 1988; Wilby et al., 2005; Casula et al., 2006) or functional synergism (Losey and Denno, 1998; Straub and Snyder, 2008). Obviously, the latter two types of interactions enhance the potential impact of predators. However, non-additive interactions also may be antagonistic and may lead to lower levels of pest suppression. This type of interaction includes intraguild predation and mutual interference (Rosenheim et al., 1995; Lang, 2003; Prasad and Snyder, 2004). Despite the potentially negative effects of intraguild predation, predator assemblages can still effectively reduce pest numbers when negative interactions occur (Snyder and Ives, 2003).

In addition to relative abundance, the taxonomic identity of predators in an assemblage also may be important because each species can vary in their effectiveness in finding, capturing and killing prey (Lundgren et al., 2006; Bologna, 2007). Depending on the differences in effectiveness among predator species in imposing mortality on prey, three intuitive yet contrasting assumptions can be made. The first is that the numerically dominant predator, regardless of taxonomic identity, imposes more prey mortality than an assemblage and is thus the key regulator of pest populations. This assumption relies on the expectation that predator abundance is tightly linked to its level of resource (prey) capture and consumption. The second assumption is that the taxonomic identity of the numerically dominant predator is important in determining whether it imposes more mortality than an assemblage. The third is that the numerically dominant predator imposes equal or less pest mortality than an assemblage. These last two assumptions suggest that (1) the numerically dominant species may be a significantly inferior predator on a given prey species (i.e., imposes less prey mortality) relative to the numerically subdominant species, (2) predator abundance is not necessarily linked to resource consumption, and (3) the foraging modes of the numerically dominant and subdominant predators may be complementary or otherwise synergistic thereby leading to positive, non-additive emergent impacts. Therefore, relative abundance and/or identity may be central factors determining the nature of interactions among multiple predator species, which in turn can enhance or diminish the ability of predator assemblages to suppress pest populations.

In this study, we investigated the importance of relative abundance and taxonomic identity of generalist species in a predator assemblage in collards (*Brassica oleracea* (Linnaeus)) on the mortality imposed on the imported cabbageworm, *Pieris rapae* (Linnaeus),

a major pest of cole crops. We tested two hypotheses, (1) regardless of identity, the numerically dominant species alone will impose greater *P. rapae* larval mortality than that imposed by an assemblage of generalist predators, and (2) the identity of the numerically dominant species determines whether it will impose greater *P. rapae* larval mortality alone than when part of an assemblage of generalist predators. Our study differs from recent works investigating the relationship between predator diversity and prey mortality in that we focus on two components of biodiversity, taxonomic identity and relative abundance. The results presented will expand our understanding of predator assemblages and their potential usefulness in management strategies such as conservation biological control.

2. Materials and methods

2.1. Sampling of foliar arthropod predators in collards

In Maryland collard fields, we found a species-rich assemblage of foliar arthropod predators that followed the pattern of relative abundance distribution described above, in that a few predator species were numerically dominant while most others were subdominant (Fig. 1, Table 1). Predators were sampled at collard (var. Vates, Meyers Seed International Inc, Baltimore, MD) plots established at the Wye Research and Education Center (Queens-

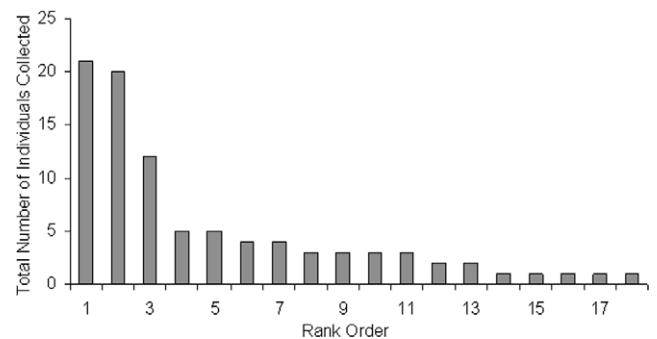


Fig. 1. Total number of foliar individuals of each species/morphospecies collected in Maryland collard fields from June–August 2004. Numbers on the x-axis represent the rank order of the species/morphospecies from most to least abundant. The names of all species/morphospecies are listed by rank order in Table 1.

Table 1

Taxonomic authorities and rank order of foliar arthropod predators collected in Maryland collard fields during June–August 2004. Underlined species refer to the predators used in this study.

Taxa	Rank order
<i>Nabis roseipennis</i>	1
<u><i>Coleomegilla maculata</i></u>	2
Tetragnathidae morphospecies 1	3
Lycosidae morphospecies 3	4
<i>Lygus lineolaris</i>	5
Araneidae morphospecies 3	6
<u><i>Coccinella septempunctata</i></u>	7
Lycosidae morphospecies 1	8
Araneidae morphospecies 2	9
Salticidae morphospecies 1	10
<u><i>Podisus maculiventris</i></u>	11
Salticidae morphospecies 2	12
<i>Chauliognathus marginatus</i>	13
Lycosidae morphospecies 2	14
Thomisidae morphospecies 1	15
Lampyridae morphospecies 1	16
<i>Tetramorium</i> sp.	17
Syrphidae morphospecies 1	18

town, Maryland) and the Central Maryland Research and Education Center at Upper Marlboro (Upper Marlboro, Maryland). At the Wye site, two conventionally tilled collard plots, each approximately 23 × 33 m, were established on May 8, 2004 and sampled from June 15 to August 2, 2004. At Upper Marlboro, two 23 × 33 m no-till plots were also established on May 8 and sampled from June 16 to July 28, 2004.

The assemblage of foliar predators was sampled by visually inspecting and hand collecting individuals found on collard plants. Ten plants were randomly selected within a 16 × 16 m area in the center of each plot at each site. Each plant was searched for a 5 min period once a week. Visual inspections typically took place between the hours of 1000 and 1200 (EST). All arthropods were collected and placed in vials with 90% ethyl alcohol and labeled by site, date, time, row, plot, and plant number. With the exception of spiders, most arthropods were identified to species or morpho-species (pending further identification). A species abundance curve was generated, with the abundances of arthropod predator species/morphospecies representing only adult individuals collected at both sites and tabulated over the entire sampling period (Fig. 1).

2.2. Study system

Coleomegilla maculata (DeGeer) was a numerically dominant foliar predator and *Coccinella septempunctata* (Linnaeus) and *Podisus maculiventris* (Say) were numerically subdominant foliar predators in sampled collards (Fig. 1 and Table 1). *C. maculata*, a native coccinellid species in North America that is predominantly found east of the midwestern states of the U.S. into southeastern Canada, is a generalist predator that feeds on aphids (Lucas et al., 2002), eggs and larvae of lepidopteran and coleopteran species (Coll and Bottrell, 1991), and supplements its diet with pollen (Cottrell and Yeargan, 1998). The coccinellid *C. septempunctata*, an introduced species (also predominantly found east of the central and midwestern states in North America) consumes several species of aphids (Biesinger and Haefner, 2005) and lepidopteran eggs and larvae (Obrycki and Orr, 1990). The native pentatomid, *P. maculiventris*, is found throughout North America and is a polyphagous predator that consumes over 90 prey species in eight insect orders (McPherson, 1980).

The imported cabbageworm, *P. rapae*, is native to Europe but is now widely distributed throughout North America and other continents. In the northeast, it is typically one of the most common herbivores in collards. Larvae are significant defoliators of collards, but are vulnerable to predation by arthropods, particularly during the first three instars (Dempster, 1967; Mauricio and Bowers, 1990).

2.3. Predator and *P. rapae* rearing

Colonies of *C. maculata*, *C. septempunctata*, *P. maculiventris*, and *P. rapae* were established in the lab. Adult *C. maculata* were obtained from a pre-existing colony established at the Insect Biocontrol Laboratory (USDA-ARS, Beltsville, MD) and were supplemented with individuals collected in the field. *C. maculata* and *C. septempunctata* adults were primarily collected from crucifer, alfalfa (*Medicago sativa* (L.)), sweet corn (*Zea mays* var. *saccharata* (L.)), small grain, and vegetable fields in Beltsville, Upper Marlboro, and Queenstown, Maryland, from May to August 2006. Some early (April 2006) collections of *C. septempunctata* adults were made in alfalfa fields in Piedmont Co., North Carolina. At all locations, predators were collected both by hand or using sweep nets. *P. maculiventris* adults were collected in the field using *Podisus* pheromone traps (developed by Jeffrey R. Aldrich, USDA-ARS, Beltsville, MD) placed in the Patuxent Wildlife Refuge and the Central Maryland Research and Education Center (both at Beltsville,

MD). *P. rapae* adults were collected in crucifer fields at the same locations in Maryland, from April to September 2006.

Predator colonies were housed in separate 0.3 m³ Plexiglas cages. Adults of all three predator species were primarily provisioned with 2nd instar *P. rapae* larvae. Substitute bee pollen (Betterbee Inc., Greenwich, NY), green peach aphids (*Myzus persicae* (Sulzer)), and Colorado potato beetle larvae (*Leptinotarsa decemlineata* (Say)) were also provided to *C. maculata*, *C. septempunctata*, and *P. maculiventris*, respectively, during periods of low *P. rapae* availability. *P. rapae* adults were placed in 1 m³ cages containing two, 6-week-old collard plants, for feeding and oviposition. Adults were provided sponges soaked in honey water. Every 2 days, collard plants were checked for newly laid *P. rapae* eggs, and egg masses were transferred to 20.3 cm diameter Petri dishes with fresh collard leaves.

2.4. Mesocosm experiments

Experimental mesocosms were used to determine the impacts of relative abundance and identity of predators on larval *P. rapae* mortality. Mesocosms consisted of 26.5 L pots (Olympia 2000, Nursery Supplies Inc., Olympia, WA) containing three, 4-week-old collard plants (var. Vates). Nineteen liter mesh bags (AZ Parts-master Co., Phoenix, AZ), supported by modified tomato trellises, were used to enclose the plants. Thirty, 1st instar *P. rapae* were placed on the leaves of the three collard plants, 10 of which were randomly placed on each plant, and allowed to settle for 24 h prior to experimentation. Ten larvae per plant represented a density that was larger than what could be consumed by each predator species in 48 h (the experimental interval), as was determined by previous feeding assay work (Moreno and Barbosa, unpublished data). Prey density was chosen to reduce the probability of underestimating the number of larvae missing as a result of predation events. Larvae were placed on mesocosm plants using paint brushes. Immediately before experimentation, each mesocosm was checked to ensure that there were a total of 30 larvae on the plants.

Six predator treatments were established in mesocosms (Table 2). Three of the treatments consisted of assemblages made up entirely of each of the three adult predator species. One assemblage (i.e., the *C. maculata* assemblage) mimicked the pattern of relative abundance found in Maryland sampled collard fields (Fig. 1), in which *C. maculata* was numerically dominant. In two other assemblages (i.e., the *C. septempunctata* and *P. maculiventris* assemblages), the species that were numerically subdominant in the field were made to be numerically dominant. The 4:1 ratio of numerically dominant to numerically subdominant individuals in the

Table 2

List of treatments, the species included in each treatment, the number of individuals per species, and the number of replicates for each treatment. C. mac. refers to *C. maculata*, C. sep. to *C. septempunctata*, and P. mac. to *P. maculiventris*. 'Assemblage' refers to treatments in which the predator is the numerically dominant species in the assemblage while 'single' refers to numerically dominant species occurring alone.

Treatment	Species included	No. of individuals per species	No. of replicates
C. mac. assemblage	<i>C. maculata</i>	4	13
	<i>C. septempunctata</i>	1	
	<i>P. maculiventris</i>	1	
C. sep. assemblage	<i>C. septempunctata</i>	4	14
	<i>C. maculata</i>	1	
	<i>P. maculiventris</i>	1	
P. mac. assemblage	<i>P. maculiventris</i>	4	12
	<i>C. maculata</i>	1	
	<i>C. septempunctata</i>	1	
C. mac. single	<i>C. maculata</i>	6	12
C. sep. single	<i>C. septempunctata</i>	6	12
P. mac. single	<i>P. maculiventris</i>	6	12

assemblage treatments was very close to the ratio of *C. maculata* to *C. septempunctata* (5:1) and *C. maculata* to *P. maculiventris* (5.7:1) individuals found in the field (Fig. 1), but still allowed us to collect sufficient individuals to conduct the experiments. The remaining three treatments represented assemblages in which each predator was the sole species in the assemblage and thus numerically dominant. We used a replacement design approach; i.e., the total number of individuals in all treatments was kept constant in all experiments.

For all treatments, individuals of the three predator species were randomly selected from their respective colonies and starved for 24 h prior to being placed on the plants in each mesocosm. All mesocosms were randomly placed into an environmental chamber set at 16L (22 °C): 8D (16 °C) and 70% RH (values that were based on the average of these environmental conditions observed during the 2004 sampling season in MD). The experiments were repeated on a weekly basis from May to September 2006 and all treatments, including the control, were replicated at least 12 times. The treatments were not replicated equally due to limitations in the amount of predators available each week, and thus varied each week. In order to avoid the loss of degrees of freedom associated with the use of a repeated measures analysis, novel plants, predators, and prey were used for each repetition of the experiment and the location of the mesocosms within the chamber was re-randomized each time.

After 48 h, *P. rapae* mortality levels were measured for each treatment by counting the number of missing/partially consumed larvae on all three plants. A control mesocosm of 30 *P. rapae* and no predators also was included to determine the background mortality of *P. rapae* larvae in the absence of predators (which was a mean of 1.9 larvae). Values for missing larvae in the predator treatments were then adjusted for the background mortality to get a more accurate assessment of the prey consumption by single predator species and predator assemblages. We also determined the expected levels of additive larval mortality among the assemblage treatments by calculating the per capita larval mortality of each species from the single treatments (e.g., *C. mac* per capita larval mortality = *C. mac* single/6), and then summing the per capita larval mortalities based on which species was numerically dominant and subdominant (e.g., *C. mac* assemblage expected additive larval mortality = *C. mac* per capita * 4 + *C. sep* per capita + *P. mac* per capita). By comparing the larval mortality levels found in the actual assemblage treatments with the expected additive values, we inferred whether the predators in assemblages likely consumed prey in an additive fashion. Current work is being conducted to statistically evaluate the actual values of larval mortality imposed by the numerically dominant and subdominant predators relative to the expected additive and non-additive values in an effort to determine the nature of the interactions exhibited in the assemblages tested here.

Following the trials, the number of *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals found alive was noted for all treatments. From this, the mean percent survival of *C. maculata*,

C. septempunctata, and *P. maculiventris* individuals (i.e., percent found alive of total starting number) was calculated for the assemblage treatments (in which these species were numerically dominant) and in single species treatments.

For the statistical analysis, predator treatments were grouped by species (factor 1) and composition type (factor 2); i.e., whether the predators were represented as single numerically dominant species or as numerically dominant species in an assemblage. The interaction between species and composition type was analyzed with a two-way ANOVA using PROC MIXED (SAS Institute, 1999). For the model, species was treated as a random effect while composition type as a fixed effect. Least square means were obtained and compared among treatments, using Tukey's multiple comparison procedure (Table 3).

2.5. Intraguild predation trials

Because intraguild predation could influence the outcome of our experiments, we determined whether any predators engage in intraguild predation. Experiments were conducted in which predators were paired without food in experimental microcosms. Microcosms consisted of a single, 15 cm tall collard plant in a 1.1 L square pot, covered by a 3.8 L mesh bag (AZ Partsmaster Co.[®]). Each pairing consisted of predator individuals of different species (starved for 24 h). After 48 h, we determined if the individual of each species was alive. A control treatment used to assess background mortality was included, in which a predator individual was placed alone in the test arena. Predators for pairing and control treatments were randomly selected from laboratory colonies. All pairing and control treatments were replicated 12 times. Differences in the mean percent survival of *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals when alone vs. when paired with other predators were compared with Fisher's Exact Test using PROC FREQ.

In addition, differences in the mean percent survival of *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals in assemblages (in which they were numerically dominant) vs. single treatments was analyzed with Kruskal–Wallis tests using PROC NPARTWAY. These analyses were conducted to determine whether there were significant differences in the survival of numerically dominant species when in an assemblage in contrast to when they were alone. Lower survivability of a numerically dominant species when in an assemblage than when alone could indicate that antagonistic interactions, such as intraguild predation, were occurring in the assemblage.

3. Results

3.1. Assemblage mesocosm experiments

There was a significant interaction effect between species and composition type ($F_{2,69} = 8.08, p < 0.01$) indicating that the impact

Table 3

Summary of planned contrasts and the treatments that were compared. *C. mac.* refers to *C. maculata*, *C. sep.* to *C. septempunctata*, and *P. mac.* to *P. maculiventris*. 'Assemblage' refers to treatments in which the predator is the numerically dominant species in the assemblage while 'single' refers to numerically dominant species occurring alone.

Planned contrast	Treatments being compared	Relevance
1. Assemblage vs. single	<i>C. mac.</i> assemblage vs. <i>C. mac.</i> single <i>C. sep.</i> assemblage vs. <i>C. sep.</i> single <i>P. mac.</i> assemblage vs. <i>P. mac.</i> single	Determines the impact of relative abundance of predators
2. Single vs. single	<i>C. mac.</i> single vs. <i>C. sep.</i> single <i>C. sep.</i> single vs. <i>P. mac.</i> single <i>P. mac.</i> single vs. <i>C. mac.</i> single	Determines the impact of taxonomic identity of predators
3. Assemblage vs. assemblage	<i>C. mac.</i> assemblage vs. <i>C. sep.</i> assemblage <i>C. sep.</i> assemblage vs. <i>P. mac.</i> assemblage <i>P. mac.</i> assemblage vs. <i>C. mac.</i> assemblage	Determines the impact of relative abundance and taxonomic identity of predators

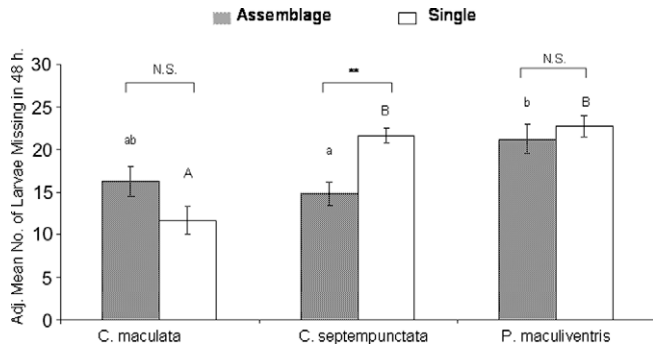


Fig. 2. Adjusted mean larval mortality (number of larvae missing in 48 h.) of the numerically dominant *Coleomegilla maculata*, *Coccinella septempunctata*, and *Podisus maculiventris* when in assemblages vs. when represented as single species. *p*-Values for contrasts between treatments were Bonferroni adjusted at the $\alpha = 0.05$ level. Data are presented as means \pm 1 SE. N.S., non significant, ** $p < 0.01$. Means with the same letter (where uppercase are for single species and lowercase for assemblage treatments) are not significantly different from each other.

of the predators was dependent on whether they were represented as single species or as an assemblage. In comparisons of assemblage vs. single treatments for each species, significantly greater larval mortality was imposed when *C. septempunctata* occurred as a single species than by an assemblage where it was numerically dominant ($t_{69} = -3.42$, $p = 0.01$; Fig. 2). For both *C. maculata* and *P. maculiventris*, there were no significant differences between assemblage and single treatment means (*C. maculata*: $t_{69} = -3.42$, $p = 0.22$; *P. maculiventris*: $t_{69} = -0.72$, $p = 0.97$).

Species identity was clearly an important determinant of the mortality imposed on *P. rapae* larvae. In comparisons of single treatments, *C. septempunctata* and *P. maculiventris* both imposed significantly greater larval mortality than *C. maculata* (*C. septempunctata*: $t_{69} = 5.09$, $p < 0.01$; *P. maculiventris*: $t_{69} = -5.43$, $p < 0.01$) but were not significantly different among each other ($t_{69} = -0.54$, $p = 0.99$; Fig. 2). Assemblages varied significantly in the mortality imposed on *P. rapae* larvae depending on which species was numerically dominant. The assemblage where *P. maculiventris* was numerically dominant imposed significantly greater larval mortality than the assemblage where *C. septempunctata* was numerically dominant ($t_{69} = -3.09$, $p = 0.03$), whereas neither of the former two assemblages imposed larval mortality that was significantly different from the assemblage where *C. maculata* was numerically dominant (*C. septempunctata*: $t_{69} = -0.72$, $p = 0.97$; *P. maculiventris*: $t_{69} = -2.37$, $p = 0.18$; Fig. 2). Furthermore, the levels of larval mortality imposed by the assemblages where *C. maculata* and *P. maculiventris* were numerically dominant were very close to their calculated expected additive values (Fig. 5). However, in the assemblage where *C. septempunctata* was numerically dominant, the larval mortality imposed was substantially less than its calculated additive value.

There was a significantly lower percentage of *C. septempunctata* individuals found alive when it was the numerically dominant species in an assemblage than when it was represented as a single species ($\chi^2(1) = 16.49$, $p < 0.01$; Fig. 3B). There were no significant differences in the percent survival when both *C. maculata* and *P. maculiventris* were the numerically dominant species in assemblages compared to their respective single treatments ($\chi^2(1) < 2.42$, $p > 0.12$; Fig. 3A and C). Intraguild predation of *C. septempunctata* by *P. maculiventris* was observed in the assemblage treatments on five occasions, four times in *C. septempunctata* assemblages, and once in the *P. maculiventris* assemblage. On one occasion, intraguild predation of *C. maculata* by *P. maculiventris* was observed in the *C. maculata* assemblage; however, no intraguild predation was observed between *C. maculata* and *C. septem-*

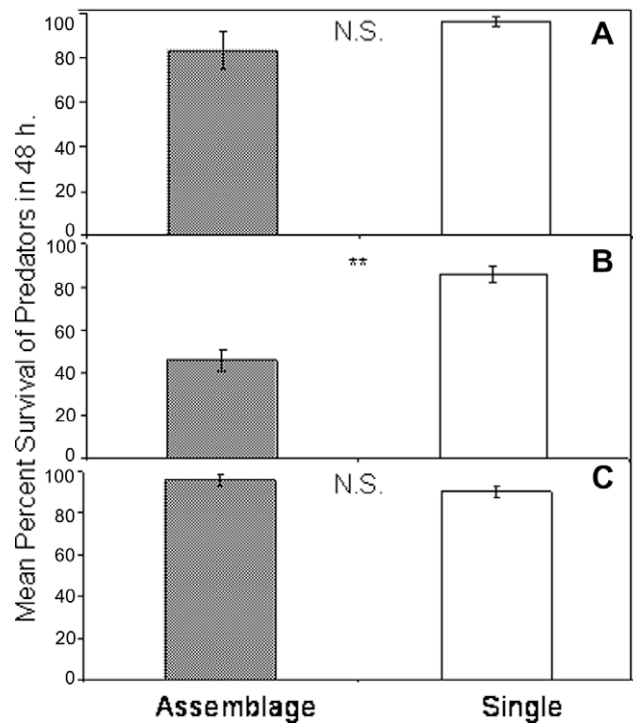


Fig. 3. Mean percent survival (% individuals found alive of total starting individuals) of (A) *Coleomegilla maculata*, (B) *Coccinella septempunctata*, and (C) *Podisus maculiventris* found in assemblage treatments (when the species is numerically dominant) vs. single treatments. N.S., non significant, ** $p < 0.01$.

punctata in any of the assemblage treatments. Cannibalism among the predators was not observed in any assemblage or single species treatments. A likely explanation for these results is provided by the experiments on intraguild predation.

3.2. Intraguild predation mesocosm trials

The intraguild predation trials confirmed that *P. maculiventris* engages in intraguild predation on *C. septempunctata*, because the mean percent survival of *C. septempunctata* individuals was significantly greater when it was alone than when it was paired with *P. maculiventris* ($\chi^2(1) = 10.99$, $p < 0.01$; Fig. 4B). When paired with *C. maculata*, the mean percent survival of *C. septempunctata* individuals was not significantly different from that observed in the single treatment ($\chi^2(1) = 0.37$, $p = 1.0$; Fig. 4B). There were no significant differences in the mean percent survival of *C. maculata* individuals when combined with *P. maculiventris* ($\chi^2(1) = 3.33$, $p = 0.22$) nor when combined with *C. septempunctata* compared to that observed in the single treatments ($\chi^2(1) = 0$, $p = 1.0$; Fig. 4A). There were also no significant differences in the mean percent survival of *P. maculiventris* individuals when combined with *C. maculata* ($\chi^2(1) = 2.14$, $p = 0.48$) nor when combined with *C. septempunctata*, compared to that observed in the single treatments ($\chi^2(1) = 0$, $p = 1.0$; Fig. 4C).

4. Discussion

Although it may be assumed that numerically dominant predators alone exert greater pest mortality than an assemblage of arthropod predators, we found evidence that this assumption depends greatly on the taxonomic identity of the numerically dominant species and their potential interactions with subdominant predators. Using an assemblage of three generalist predators found in collards, we found that only when *C. septempunctata*, a numeri-

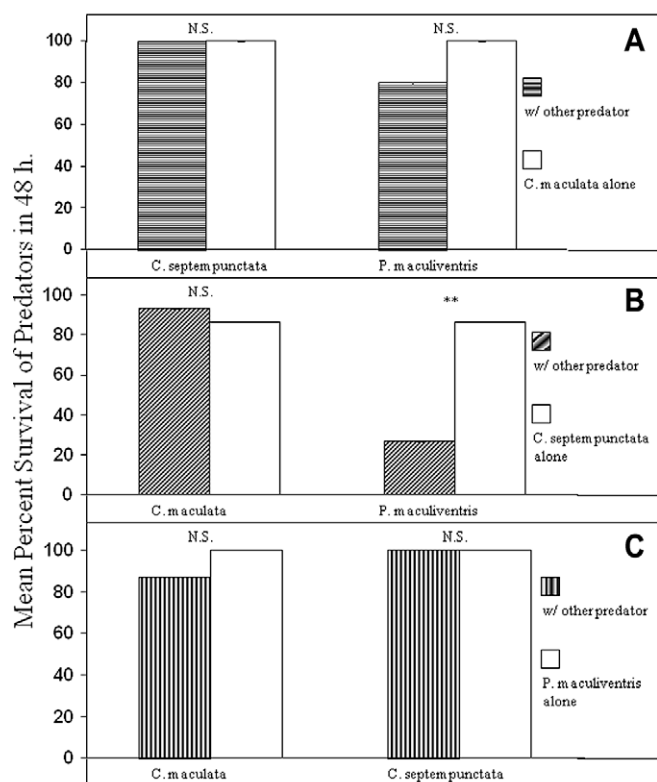


Fig. 4. Mean percent survival of (A) *Coleomegilla maculata*, (B) *Coccinella septempunctata*, and (C) *Podisus maculiventris* individuals (% individuals found alive in 48 h.) when paired with individuals of other predator species vs. when alone. N.S., non significant, $^{**} p < 0.01$.

cally subdominant predator in the field, was made a numerically dominant species, did the most abundant species alone impose greater *P. rapae* larval mortality than when in an assemblage (Fig. 2). On the other hand, when both *C. maculata* (the numerically dominant species in the field) and *P. maculiventris* (a numerically subdominant species in the field) were made numerically dominant, the levels of larval mortality imposed by these species alone were similar to the larval mortality imposed when they were in

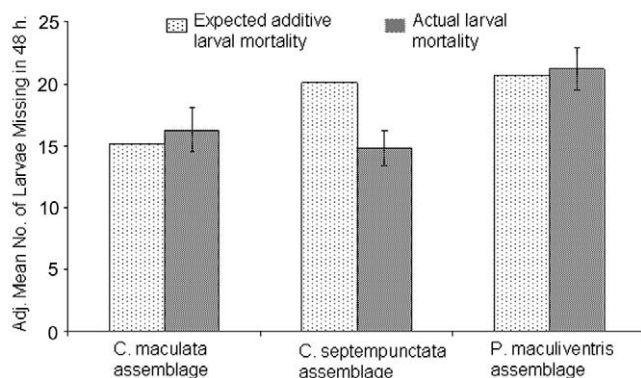


Fig. 5. A comparison of the expected additive larval mortality vs. the actual mean larval mortality (number of missing larvae in 48 h) imposed by assemblages where *Coleomegilla maculata*, *Coccinella septempunctata*, and *Podisus maculiventris* were the numerically dominant species. Expected additive mortality for assemblages was determined by calculating the larval mortality imposed by each species from the single treatments, and then summing the per capita larval mortalities based on which species is numerically dominant and subdominant in assemblages.

assemblages. These results support the hypothesis that taxonomic identity, and not abundance per se, is important in determining whether numerically dominant species impose greater larval *P. rapae* mortality alone than when in an assemblage of generalist predators.

The importance of taxonomic identity is supported by a concurrent study using the same predator and prey species that demonstrated that predator species identity altered the relationship between predator species richness and prey mortality (Lewins and Barbosa, unpublished data). The results of Lewins and Barbosa (unpublished data) showed that larval mortality of *P. rapae* did not linearly increase with greater species richness per se, but was contingent on the taxonomic identity of the predator species added. As important as predator species identity may be, the type of interactions that occur among numerically dominant and subdominant species also may be crucial in determining the impact of the most abundant species in a predator assemblage. While not explicitly tested in our study, we were able to deduce the nature of interactions that occurred among some of these predators by independently analyzing the impacts of single species and assemblages on herbivore mortality. Although they imposed similar levels of larval *P. rapae* mortality, *P. maculiventris* and *C. septempunctata* were both more effective at imposing larval mortality than *C. maculata* as individual species (Fig. 2). This indicates that there were identity-based differences in prey consumption. However, in assemblages, there was a significant drop-off in larval mortality when *C. septempunctata* was numerically dominant compared to when *P. maculiventris* was numerically dominant (Fig. 2). Further, when *C. maculata* was numerically dominant, the level of larval mortality imposed by the assemblage was not distinguishable from that of the other two assemblages.

The difference in the impacts of single predator species vs. the species in assemblages suggests that interactions among numerically dominant and subdominant species influenced the impact they had on *P. rapae* mortality. If interactions among the species had been strictly additive, then the larval mortality imposed by assemblages should have been equal to the summed impacts of the individual numerically dominant and subdominant species. However, the larval mortality imposed by the assemblages did not appear to be additive for all of the numerically dominant/subdominant combinations (Fig. 5). The comparison suggests that while interactions in assemblages where *C. maculata* and *P. maculiventris* were numerically dominant likely resulted in additive consumption of *P. rapae*, they appear to have been antagonistic in assemblages where *C. septempunctata* was the numerically dominant species, resulting in a level of larval mortality that was less than additive. We realize that a more rigorous comparative approach is needed to properly analyze the expected additive versus observed larval mortality impacts of assemblages, and to more accurately determine the interactions among *C. maculata*, *C. septempunctata*, and *P. maculiventris*. As noted in the Materials and methods section, we are currently developing an analysis that will not only allow us to compare the expected additive and observed impacts of the predators used in this study, but also to predict the impacts of other species found in the sampled assemblage of foliar predators in Maryland collard fields that were not included in this study.

Intraguild predation was the most likely cause of the antagonistic interactions occurring in the assemblages where *C. septempunctata* was the numerically dominant species, as we found that *P. maculiventris* was an asymmetric intraguild predator of *C. septempunctata* in separate trials (Fig. 4B). These results concur with the growing body of literature indicating that antagonistic interactions in predator assemblages, such as intraguild predation, can lead to a reduction in pest mortality (Polis et al., 1989; Rosenheim et al., 1993, 1995; Snyder and Ives, 2001; Finke and Denno, 2004,

2005). However, our research expands on this theme by showing that intraguild predation by a numerically subdominant species, *P. maculiventris*, can represent a significant source of mortality on a numerically dominant species, in this case *C. septempunctata*. This, in turn, may substantially alter the potential impact of a numerically dominant predator on prey. On the other hand, the level of prey mortality imposed by an effective intraguild predator, such as *P. maculiventris*, when it is numerically dominant, may not be substantially reduced in the presence of a numerically subdominant intraguild prey like *C. septempunctata*. Therefore, the relative abundances of predators may be an important component in determining the outcomes and impacts of intraguild predation on pest mortality.

Our findings thus indicate that the impact of numerically dominant predators on prey mortality can be influenced by their relative abundance, their identity, and their interactions with numerically subdominant species. Furthermore, the results of our study have important implications to the ongoing evaluation of the relationship between predator diversity and resource consumption, or in this case, prey mortality. The ample occurrence of all three outcomes (i.e., positive, negative, neutral relationships) in the literature suggests that the nature of multi-enemy impacts is context dependent (Finke and Denno, 2005; Wilby et al., 2005; Cardinale et al., 2006; Cakmak et al., 2009). However, there is also substantial evidence to date that natural enemy assemblages are no more effective at imposing prey mortality than single effective species (Schmitz, 2007; Straub and Snyder, 2006, 2008; but see Letourneau et al., 2009). The results of our study support and further build upon this evidence by showing that multi-predator effects among species that vary in (a) relative abundance and (b) effectiveness in imposing prey mortality were not stronger than that of single species. This is particularly noteworthy in the assemblage where *C. maculata* was numerically dominant, given that the inclusion of two highly effective subdominant predators (*C. septempunctata* and *P. maculiventris*) did not produce significantly greater levels of prey mortality relative to the lowly effective numerically dominant predator alone. Thus, our results suggest that while (1) the lack of positive, non-additive impacts among multiple predators may be at least partially due to the rarity and thus low impacts of subdominant species relative to numerically dominant ones, (2) the potential for antagonistic, non-additive impacts may be high with the inclusion of subdominant intraguild predators, in spite of their rarity and high relative effectiveness in imposing pest mortality. More studies are needed at the field level to determine the prevalence of antagonistic and complementary interactions among numerically dominant and subdominant predators, and their potential additive and non-additive impacts on prey suppression.

We recognize that intraguild predation among the immature stages of these predators may differ and also play a role in the impacts of assemblages on prey species. To experimentally sort out and differentiate all the permutations of adult and all immature stages of even three species would likely be unwieldy and perhaps uninformative, if even possible. Nevertheless, implicit in our results is that effective management of pest populations may be achieved through the conservation of a numerically dominant predator, albeit with two major caveats. The first caveat is that this result may be dependent on species identity, as the numerically dominant species in the field may not be the most effective predator. The second caveat is that the impact of the numerically dominant predator on prey mortality may be diminished by the presence of numerically subdominant intraguild predators. If the numerically dominant predator in the field is not the most effective species in the assemblage, then numerically subdominant species may not provide a significant added source of prey mortality. Consequently, if conservation biological control tactics are to be

employed, an in-depth understanding of key natural enemy assemblages is required to determine which assemblage is likely to work best against which pest.

Acknowledgments

We thank Drs. Jeffrey R. Aldrich, Don Weber, and Zsofia Szendrei, and the Insect Biocontrol Laboratory (USDA-ARS, Beltsville, MD) for their assistance in establishing lab colonies of all the predators used in this study, Mike Newell, Kevin Conover, Mark Spicknall at the Central, Wye, and Upper Marlboro, Maryland Research and Education Centers, respectively, for their assistance in preparation of the field sites used for collecting specimens, Steve Bambara, Kenneth Snyder, Charlie Campbell, and Galen Dively for their assistance in finding sites in which to collect the species needed for this research, and Dr. Robert Denno, Dr. Galen Dively, Dr. Astrid Caldas, Dr. John Kemper, Dr. Raul Medina, Dr. Deborah Letourneau, Dr. Eric Lind, Dr. Joy Hagan, Gwen Shlichta, Megan Paustian, Sara Bothwell Allen, Julie Jedlicka, and Timothy Krupnik, for their valuable comments and suggestions on the original manuscript. We also thank Antti Koskelo, Hau Phan, Diana Do, Nat Lichten, Kayur Shah, Christine Sunkler, Donald Grant, and Samantha Whitehead for their help in collecting field and lab data. This study was supported by a grant from the Cosmos Club Foundation.

References

- Barbosa, P., 1998. Conservation Biological Control. Academic Press, San Diego.
- Barbosa, P., Caldas, A., Reichert, S.E., 2005. Species abundance distribution and predator–prey interactions: theoretical and applied consequences. In: Barbosa, P., Castellanos, I. (Eds.), Ecology of Predator–Prey Interactions. Oxford University Press, New York, pp. 344–369.
- de Bello, F., Leps, J., Lavorel, S., 2007. Importance of species abundance for assessment of trait composition: an example based on pollinator communities. *Community Ecology* 8, 163–170.
- Biesinger, Z., Haefner, J.W., 2005. Proximate cues for predator searching: a quantitative analysis of hunger and encounter rate in the ladybird beetle, *Coccinella septempunctata*. *Animal Behaviour* 69, 235–244.
- Bologna, P.A.X., 2007. Impact of differential predation potential on eelgrass (*Zostera marina*) faunal community structure. *Aquatic Ecology* 41, 221–229.
- Cakmak, I., Janssen, A., Sabelis, M.W., Baspinar, H., 2009. Biological control of an acarine pest by single and multiple natural enemies. *Biological Control* 50, 60–65.
- Cardinale, B.J., Harvey, C.T., Gross, K., Ives, A.R., 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* 6, 857–865.
- Cardinale, B.J., Weis, J.J., Forbes, A.E., Tilmon, K.J., Ives, A.R., 2006. Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator–prey system. *Journal of Animal Ecology* 75, 497–505.
- Casula, P., Wilby, A., Thomas, M.B., 2006. Understanding biodiversity effects on prey in multi-enemy systems. *Ecology Letters* 9, 995–1004.
- Chang, G.C., Kareiva, P., 1999. The case for indigenous generalists in biological control. In: Hawkins, B.A., Cornell, H.V. (Eds.), Theoretical Approaches to Biological Control. Cambridge University Press, Cambridge, pp. 103–115.
- Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M., Hormiga, G., 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology* 78, 573–584.
- Coll, M., Bottrell, D.G., 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland field corn. *Environmental Entomology* 20, 526–533.
- Cottrell, T.E., Yeargan, K.V., 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* 27, 1402–1410.
- Dempster, J.P., 1967. The control of *Pieris rapae* with DDT 1: the natural mortality of the young stages of *Pieris*. *Journal of Applied Ecology* 4, 485–500.
- Finke, D.L., Denno, R.F., 2004. Predator diversity dampens trophic cascades. *Nature* 429, 407–410.
- Finke, D.L., Denno, R.F., 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8, 1299–1306.
- Finke, D.L., Snyder, W.E., 2008. Niche partitioning increases resource exploitation by diverse communities. *Science* 321, 1488.
- Holland, J.M., Thomas, S.R., Hewitt, A., 1996. Some effects of polyphagous predators on an outbreak of cereal aphid (*Sitibion avenae* F.) and orange wheat blossom midge (*Sitodiplosis mosselana* Gehin). *Agriculture, Ecosystems, and Environment* 59, 181–190.
- Lang, A., 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* 134, 144–153.

- Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 40, 573–592.
- Losey, J.E., Denno, R.F., 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79, 2143–2152.
- Lucas, E., Gagne, I., Coderre, D., 2002. Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 99, 457–463.
- Lundgren, J.G., Shaw, J.T., Zaborski, E.R., Eastman, C.E., 2006. The influence of organic transition systems on beneficial ground-dwelling arthropods and predation of insects and weed seeds. *Renewable Agriculture and Food Systems* 21, 227–237.
- Mauricio, R., Bowers, M.D., 1990. Do caterpillars disperse their damage? Larval foraging behaviour of two specialist herbivores, *Euphydryas phaeton* (Nymphalidae) and *Pieris rapae* (Pieridae). *Ecological Entomology* 15, 153–161.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10, 995–1015.
- McPherson, J.E., 1980. A list of the prey species of *Podisus maculiventris* (Hemiptera: Pentatomidae). *Great Lakes Entomology* 13, 17–24.
- Novotny, V., Basset, Y., 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89, 564–572.
- Obrycki, J.J., Orr, C., 1990. Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera:Coccinellidae). *Journal of Economic Entomology* 83, 1292–1297.
- Paarmann, W., Adis, J., Stork, N., Gutzmann, B., Stumpe, P., Staritz, B., Bolte, H., Koppers, S., Holzkamp, K., Niers, C., Da Fonseca, C.R.V., 2001. The structure of ground beetle assemblages (Coleoptera: Carabidae) at fig fruit (Moraceae) in a terra firme rain forest near Manaus (Brazil). *Journal Tropical Ecology* 17, 549–561.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20, 297–330.
- Prasad, R.P., Snyder, W.E., 2004. Predator interference limits fly egg biological control by a guild of ground active beetles. *Biological Control* 31, 428–437.
- Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological-control agents: theory and evidence. *Biological Control* 5, 303–335.
- Rosenheim, J.A., Wilhoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist predators on the suppression of an herbivore population. *Oecologia* 96, 439–449.
- SAS institute, 1999. SAS user's guide, version 8. SAS institute, Cary, North Carolina.
- Schmitz, O.J., 2007. Predator diversity and trophic interactions. *Ecology* 88, 2415–2426.
- Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., Sartanto, P., 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77, 1975–1988.
- Snyder, G.B., Finke, D.L., Snyder, W.E., 2008. Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities. *Biological Control* 44, 52–60.
- Snyder, W.E., Ives, A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82, 705–716.
- Snyder, W.E., Ives, A.R., 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84, 91–107.
- Snyder, W.E., Snyder, G.B., Finke, D.L., Straub, C.S., 2006. Predator biodiversity strengthens herbivore suppression. *Ecology Letters* 9, 789–796.
- Soluk, D.A., Collins, N.C., 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among predators. *Oikos* 52, 94–100.
- Straub, C.S., Snyder, W.E., 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology* 87, 277–282.
- Straub, C.S., Snyder, W.E., 2008. Increasing enemy biodiversity strengthens herbivore suppression on two plant species. *Ecology* 89, 1605–1615.
- Straub, C.S., Finke, D.L., Snyder, W.E., 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control* 45, 225–237.
- Sugihara, G., 1980. Minimal community structure – an explanation of species abundance patterns. *American Naturalist* 116, 770–787.
- Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47, 561–594.
- Ulrich, W., 2005. Regional species richness of families and the distribution of abundance and rarity in a local community of forest Hymenoptera. *Acta Oecologica – International Journal of Ecology* 28, 71–76.
- Wilby, A., Villareal, S.C., Lan, L.P., Heong, K.L., 2005. Functional benefits of predator species diversity depend on prey identity. *Ecological Entomology* 30, 497–501.