



# Pairwise interactions between functional groups improve biological control



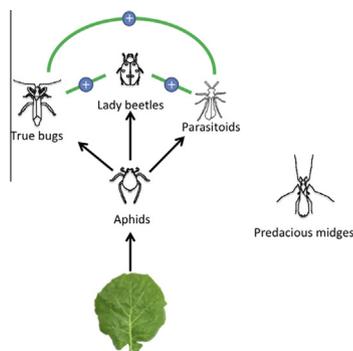
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## HIGHLIGHTS

- An approach combining advantages of substitutive and additive designs is introduced.
- Combining predator functional groups improved biological control.
- There was no evidence of disruptive interactions between predators.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Ecologists have long debated whether predators primarily disrupt one another's prey capture through interspecific interference, or instead complement one another by occupying different feeding niches. Resolution of this debate has been difficult because different experimental designs are typically used to study interference versus complementarity. We adopted a somewhat atypical approach, surveying communities of predatory insects on 73 free-growing *Brassica oleracea* plants, and then re-constructing each community in field cages to measure its impact on aphid prey. The predator communities naturally varied in species composition, richness, and relative abundance; in our experiment we kept total predator density constant to avoid confounding effects of differing overall abundance. The predator communities' impacts on aphids differed by >10-fold. Using a generalized linear model, we found that pairings of several predators in the community improved aphid suppression while no pairings disrupted it. Indeed, accounting for the presence of the beneficial pairings provided more power than species richness to explain predators' impacts on aphids. Altogether, our results suggest generally complementary or neutral, rather than disruptive, multi-predator effects in this community. Our approach may be useful for determining the frequency of complementary species-pairings in many other systems.

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## 1. Introduction

Ecologists have long debated whether different predator species act together to suppress herbivore populations, or instead interfere with one another (Ives et al., 2005; Polis et al., 1989; Sih et al., 1998). Early work suggested that predator species generally form either one coherent third trophic level (e.g., Hairston et al., 1960;

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Oksanen et al., 1981), or separate third and fourth trophic levels (Power, 1990) that act together to impact prey at distinctly-separate trophic levels. Subsequently, it was pointed out that predators often feed on one another, blurring distinctions among trophic levels and perhaps generally weakening predators' top-down impacts on herbivores (Polis et al., 1989). Most recently, ecologists interested in the relationship between biodiversity and biological control have often found evidence of predators occupying different niches and thus complementing one another (Straub et al., 2008; Bruno and Cardinale, 2008; Letourneau et al., 2009). When predators are complementary, the combined impact of multiple predator species on prey exceeds that of any single predator species (e.g., Finke and Snyder, 2008). Heated debate has at times erupted among camps focusing on intraguild predation versus complementarity (e.g., Hairston and Hairston, 1993; Polis and Holt, 1992), while synthetic treatments have variously found support for primarily disruptive (Polis et al., 1989), neutral (Halaj and Wise, 2001; Schmitz, 2007), or complementary (Cardinale et al., 2006; Letourneau et al., 2009) impacts of multiple predator species.

One complication in resolving this debate is the often very different experimental designs used by ecologists interested in predator interference versus those examining predator complementarity (Ives et al., 2005; Sih et al., 1998). Studies of predator interference generally hold densities of each predator species constant across richness levels, isolating the effects of interspecific interactions by holding intraspecific interactions constant (Byrnes and Stachowicz, 2009; Ives et al., 2005; Sih et al., 1998). These additive designs generally include relatively small numbers of predator species, because total predator densities at the highest species-richness levels rapidly escalate as more species are added. Analyses generally use per capita effects of each predator alone to predict effects of multiple predators, and compare experimental results to these predictions (Sih et al., 1998). In contrast, studies of predator complementarity often use substitutive designs, where total predator density is held constant as more species are added, which allows for the inclusion of relatively large numbers of species typical of some predator communities (e.g., Bruno and O'Connor, 2005; Northfield et al., 2012). These predator complementarity studies generally compare prey consumption by diverse communities to the average consumption by single species treatments (e.g., Snyder et al., 2006). Thus the per capita contribution by each predator species is generally not a focus of the analysis. This has led to concerns over "sampling" or "species identity" effects and the development of *post hoc* analyses that attempt to account for these effects (e.g., Loreau, 1998).

Here, we deployed a hybrid approach that combined elements of both substitutive and additive manipulations of predator biodiversity. We did this by joining a manipulation of predator species-composition and relative density at a constant overall predator density (typical of a substitutive design), followed by analyses using generalized linear model to compare predation by diverse communities to predictions drawn from per capita effects of each species (typical of an additive design). First, we documented the structure of insect-predator communities that had naturally assembled in the open field, attacking aphids on *Brassica oleracea* L. plants. We then reproduced each predator assemblage found on a particular plant in field cages where we could isolate and quantify impacts of each predator community on aphid consumption by incorporating the densities of each species into a generalized linear model. These predator-impact data then were used to determine, using a generalized linear model, whether pairs of predator species typically interfered with or complemented one another. This approach allowed us to include relatively large numbers [compared to the two or three species often included in additive designs (Sih et al., 1998)] of predator species (as often accomplished within substitutive manipulations of predator

species richness) while also measuring both single species' impacts and the combined impacts of predator species pairs (as often accomplished within additive manipulations of species richness).

## 2. Materials and methods

### 2.1. Natural history

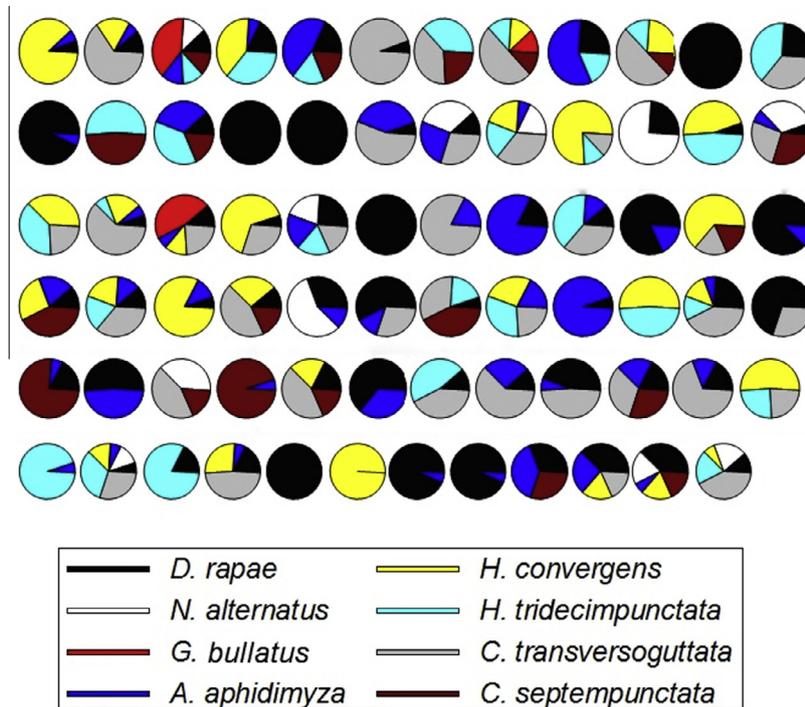
Our experiments focused on the community of predatory insects attacking *Brevicoryne brassicae* L. aphids on *B. oleracea* plants in Washington, USA. Common predator species include several species of predatory bugs, lady beetles and flies, along with parasitoid wasps (Table A.1, Fig. 1; Snyder et al., 2006). Pairs of species in this community variously occupy distinct spatial niches and thus complement one another (e.g., Gable et al., 2012), and/or prey upon one another and thus disrupt one another's feeding (e.g., Snyder et al., 2006). Despite the potential for both positive and negative multi-predator effects in this system, a series of predator-richness manipulations has consistently revealed increasing aphid suppression with greater predator species richness (Gable et al., 2012; Northfield et al., 2010; Straub and Snyder, 2008). However, earlier experiments have typically used traditional substitutive designs and analyses, such that predator community structure was manipulated to ease the isolation of species-richness effects, rather than identify particularly important pairings of individuals. The work reported here expands upon our earlier findings by constructing predator communities to reproduce those found on aphid-infested *B. oleracea* plants growing naturally in the field. This approach allows us to use a generalized linear model framework that combines the benefits of both substitutive and additive designs.

### 2.2. Field survey of predator-community structure

To determine the structure of naturally-occurring predator communities, we visually surveyed the arthropods living on *B. oleracea* plants growing unconstrained in the field. Plots of *B. oleracea* plants were established by transplanting 4-week-old seedlings (started in a greenhouse at 16:8 h photoperiod) into three plots at Washington State University's Tukey Horticultural Orchard in Pullman, Washington, USA, on 15 May 2008. Each plot included 10 rows of 10 plants, covering 8 × 8 m, with plots separated from each other by 8 m of bare ground. Plants were irrigated as needed but otherwise left un-disturbed, and were naturally colonized by both *B. brassicae* aphids and their predators. Insect assemblages on these plants were surveyed on 31 July 2008, roughly coinciding with the seasonal peak in insect activity (Gable et al., 2012).

In each of the three plots, every-other plant was sampled in every-other row, such that 25 plants were sampled from each plot (5 rows × 5 plants/row × 3 plots = 75–2 plants that had died = 73 plants total). During the survey we first conducted timed, 1-min searches of the entire plant during which we recorded all predators observed. Lady beetle larvae could not be visually attributed to species. Next, we divided the plant into thirds, consisting of the newest leaves, oldest leaves, and middle-aged leaves, and counted the number of aphids, aphids observed to contain pupae of parasitoid wasps ("mummies"), and larval *Aphidoletes aphidimyza* Rondani, on two randomly selected leaves from each plant section; a count of the total number of leaves allowed us to estimate the number of parasitoids and *A. aphidimyza* per plant.

Our survey data recorded the number of juvenile *Diaeretiella rapae* (McIntosh) and *A. aphidimyza* only, because adults of both species are small, highly mobile, and difficult to count. In the field-cage experiment, to establish densities of reproductive females of each of these two species equivalent to what was



**Fig. 1.** Initial proportional composition of each predator assemblage used in the analysis, each of which included some combination of *Nabis alternatus*, *Geocoris bullatus*, *Hippodamia convergens*, *H. tridecimpunctata*, *Coccinella transversoguttata*, *C. septempunctata*, *Diaeretiella rapae*, and/or *Aphidoletes aphidimyza*. Pie charts are in descending order (left to right, top to bottom) of final aphid densities for each community included in the field-cage experiment. One extreme outlier (community #53, Table A.1) was removed from the analysis, for which aphid densities were 5.6 times greater than the mean density in the no-predator controls (426 aphids/plant).

recorded in the open field, we calculated the expected number of adult females of each species by dividing mummy and larval midge counts by the published reproduction rate for each (*D. rapae*: 229 larvae per female (Hsieh and Allen, 1986); *A. aphidimyza*: 150 larvae per female (Gilkeson, 1987).

### 2.3. Relating predator-community structure to impacts on prey

Next, we estimated the impact on aphids of each of the 73 different plant-specific predator assemblages found in the field survey (Table A.1, Fig. 1), by reconstructing each of the 73 communities in a separate field cage. This field experiment was necessary because each community's impact on aphids could not be ascertained from the field survey alone. Field cages were  $2 \times 2 \times 2\text{-m}$  ( $8\text{-m}^3$ ) and constructed as previously described (Snyder et al., 2006), each housing four 4-week-old *B. oleracea* plants transplanted from the greenhouse (described above) on 24 July 2009. Four days later, each plant was infested with 20 aphids (80 aphids per cage), collected from an aphid colony maintained in a field cage (as in Snyder et al., 2006), and predators were released 72 h later. Our *B. brassicae* field colony was contaminated with small numbers of a second aphid species, *Myzus persicae*, and thus our analyses focused on total aphid density summed across both species.

Total predator densities were held constant at 4 individuals per plant (16 per cage), approximating the mean per-plant density seen in the field survey (mean  $\pm$  SE:  $3.89 \pm 0.36$ ). For each cage, the proportion of each predator species found on the field-surveyed plant serving as that cage's model "real" community was multiplied by 16 to determine the number of predator individuals to add to that cage, rounding to the nearest whole number to avoid the gruesome task of cutting individual predators into fractions (Table A.1; see also Crowder et al., 2010). All predators were added as adults collected from surrounding vegetation, with the

exception of *D. rapae*, which came from a field colony (as in Snyder et al., 2006). In addition to the 73 cages housing predators, we also established five no-predator controls housing only aphids and plants.

First just before predator release, and then four weeks later, we counted all insects found on two randomly selected plants per cage. At the 4-week count, parasitoids were in their second generation, and at the pupal (mummy) stage that is readily identifiable.

### 2.4. Analysis

Typically, within substitutive designs all predator species are held equally likely to co-occur with one another at equal relative abundances (Huston, 1997). To measure the divergence of our field populations from these ideals, we conducted Pearson's correlation tests of the arcsine-square-root-transformed abundances of all predator species to one another. Pearson's correlation tests were conducted in SAS (proc corr, Version 9.3, SAS Institute, 2012).

We used a generalized linear model framework (proc genmod, Version 9.3, SAS Institute, 2012) to assess predator impacts on aphids in our field-cage experiment. Our statistical model included each predator species' density and its pairwise interactions with each other predator species; these interaction terms examined whether predators combined to increase (positive interaction) or decrease (negative interaction) overall aphid consumption. The full model including the intercept, a density effect for each species (8 total; see Section 3), each pairwise species interaction and species richness totaled 36 parameters. Therefore, we evaluated combinations of redundant predators that could be evaluated as one group to reduce the number of parameters in the model. Aphid counts fit a negative binomial distribution; this distribution allows a log link function that accounts for multiplicative effects of multiple predators in a way analogous to that suggested by Sih et al. (1998). One extreme outlier (community #53, Table A.1) was removed from the

analysis, for which aphid densities were 5.6 times greater than the mean density in the no-predator controls (426 aphids/plant). To reduce the number of the parameters in the model we evaluated models that grouped species by family or order, and compared the AICc values of each simplified model to the full model. We use the AICc, rather than AIC, because this metric explicitly considers sample size when assessing models. AICc accomplishes this through an added correction term,  $2(m+1)(m+2)/(n-m-2)$ , where  $m$  and  $n$  are the number of model parameters, and the sample size, respectively; this term magnifies the penalty for extra parameters when sample sizes are small (Hurvich and Tsai, 1989).

### 3. Results

#### 3.1. Field survey of predator-community structure

Eight predator species were found on *B. oleracea* plants in our open-field plots (Table A.1): the predatory bugs *Nabis alternatus* Parshley and *Geocoris bullatus* (Say); the lady beetles *Hippodamia convergens* (Guerin-Meneville), *Hippodamia tridecimpunctata* L., *Coccinella transversoguttata* Brown, and *Coccinella septempunctata* L.; the parasitoid wasp *D. rapae* (McIntosh); and the predacious midge *A. aphidimyza* Rondani. The pupae of the parasitoid were relatively uncommon in the presence of other predators, and thus parasitoid abundance was negatively correlated with the densities of each lady beetle species and with predator species richness (Table 1). Likewise, there was a significant negative correlation between the density of the lady beetle *H. convergens* and that of *A. aphidimyza* (Table 1). In contrast, all true predator species other than *A. aphidimyza* were more abundant in predator communities that included more species (Table 1).

#### 3.2. Relating predator-community structure to impacts on prey

Predator communities varied widely in their effects on aphids (Fig. 1). We found that combining the densities of the four species of lady beetles (*H. convergens*, *H. tridecimpunctata*, *C. transversoguttata*, and *C. septempunctata*) into one parameter, and the densities of the true bugs (*G. bullatus* and *N. alternatus*) into another parameter, each improved the fit of the generalized linear model to the data. Combining true bugs and lady beetles provided a better fit than either only combining lady beetles ( $\Delta\text{AICc} = 6.55$ ), only combining true bugs ( $\Delta\text{AICc} = 35.33$ ), or not combining any species ( $\Delta\text{AICc} = 40.85$ ). This suggests that each member species of the “true bugs” and “lady beetle” groupings represented relatively redundant species. We included species number in our models (Table 2). Including a term describing the number of functional groups (i.e., with the two bug species lumped, and with the four lady beetle species lumped), rather than the number of species, changed model fit only slightly ( $\Delta\text{AICc} = 0.72$ ); thus, conducting

**Table 2**

Generalized linear model outputs describing the effects of species richness (Sp), the densities of *Diaretiella rapae* (Dr), *Aphidoletes aphidimyza* (Aa), lady beetles (combined densities of *Hippodamia convergens*, *Hippodamia tridecimpunctata*, *Coccinella transversoguttata*, and *Coccinella septempunctata*) (Lb), true bugs (combined densities of *Geocoris bullatus* and *Nabis alternatus*) (Bugs), and pairwise interactions between the densities of each predator group, on final aphid densities in the field-cage experiment. Negative estimates indicate that increased densities of the particular species or combination of species reduced experimental aphid densities. Each parameter is estimated only after accounting for all other parameters. Combining true bugs and lady beetles provided a better fit than either only combining lady beetles ( $\Delta\text{AICc} = 6.55$ ), only combining true bugs ( $\Delta\text{AICc} = 35.33$ ), or not combining any species ( $\Delta\text{AICc} = 40.85$ ). Error degrees of freedom = 64. We assumed a negative binomial error distribution in aphid counts.

Parameter	DF	Estimate	Wald $\chi^2$	Pr > ChiSq
Aa	1	-0.064	0.44	0.507
Dr	1	-0.086	4.82	0.028*
Lb	1	-0.102	4.41	0.036*
Bugs	1	0.734	5.16	0.023*
Aa × Dr	1	-0.019	1.02	0.311
Aa × Lb	1	-0.002	0.02	0.876
Aa × Bugs	1	0.038	0.63	0.426
Dr × Lb	1	-0.022	5.48	0.019*
Dr × Bugs	1	-0.212	7.23	0.007*
Lb × Bugs	1	-0.096	7.67	0.006*
Sp	1	0.248	1.48	0.224

\* Asterisks indicate significance at  $\alpha = 0.05$ .

analyses with either species number or functional group number produced qualitatively similar results.

Greater densities of the parasitoid *D. rapae* and the combined lady beetle species correlated with lower final aphid densities, and these species' combined effects further increased aphid suppression (Table 2). On their own true bugs did not reduce aphid densities, but these predators combined with lady beetles and the parasitoid to enhance aphid suppression (Table 2). When these interactions were not included in the model true bugs had no positive or negative affect (data not shown), but after accounting for this interspecific complementarity the statistical model predicted increased aphid densities in the presence of true bugs alone (Table 2). After accounting for the main and interactive effects of these three highly-impactful taxa (*D. rapae*, lady beetles and true bugs) on aphids, species richness itself provided no additional explanatory power (Table 2). The fly *A. aphidimyza* had no significant individual or interactive effect on aphid densities (Table 2).

### 4. Discussion

Predator assemblages constructed to reproduce those found on *B. oleracea* plants in the field varied widely in their impacts on aphids. These differences appeared to reflect two factors: (1) the presence of particularly impactful single predator species and (2)

**Table 1**

Pearson's correlation coefficients for pairwise correlations of the relative abundances among *Diaretiella rapae* (Dr), *Nabis alternatus* (Na), *Geocoris bullatus* (Gb), *Hippodamia convergens* (Hc), *Hippodamia tridecimpunctata* (Ht), *Coccinella transversoguttata* (Ct), *Coccinella septempunctata* (Cs), *Aphidoletes aphidimyza* (Aa), and species richness (Richness) in the field survey of 73 collard plants in Othello, WA. Asterisks designate correlation coefficients significantly different from zero ( $\alpha = 0.05$ ).

	Dr	Na	Gb	Hc	Ht	Ct	Cs	Aa
Dr	-	-	-	-	-	-	-	-
Na	-0.100	-	-	-	-	-	-	-
Gb	-0.067	0.038	-	-	-	-	-	-
Hc	-0.510*	-0.149	0.000	-	-	-	-	-
Ht	-0.492*	-0.089	-0.013	0.115	-	-	-	-
Ct	-0.458*	0.055	0.044	0.067	0.026	-	-	-
Cs	-0.255*	0.028	0.042	-0.131	-0.018	-0.057	-	-
Aa	-0.030	-0.059	-0.018	-0.270*	-0.112	-0.085	-0.055	-
Richness	-0.491*	0.254*	0.335*	0.210	0.281*	0.497*	0.292*	0.073

pairings of predator species that combined to enhance aphid suppression. A parasitoid wasp and lady beetles each exerted both individually-strong impacts on aphids, and combined to suppress aphids more than would be predicted based on their individual impacts (Table 2). On their own, predatory bugs did not reduce aphid densities, but these predators combined with either lady beetles or the parasitoid wasp to enhance aphid suppression (Table 2). Redundancy among some species also may be present, as the fit of statistical models was improved when the two predatory bug species, *G. bullatus* and *N. alternatus*, were lumped together, and also when the four lady beetle species were considered as one (Table 2). The predatory fly *A. aphidimyza* neither impacted aphids on its own, nor impacted predation when paired with other predator species (Table 2). We saw no evidence that predator species interfered with one another's prey capture, as no species pairing led to weaker aphid suppression (Table 2). Rather, widespread positive predator–predator interactions suggested that most species either complemented one another (e.g., Gable et al., 2012) or synergistically enhanced one another's prey capture (e.g., Losey and Denno, 1998). Thus, multi-predator effects either improved or were neutral to the overall strength of herbivore suppression, and never disrupted it.

Some of the best-known examples of predator–predator interference that weakens herbivore suppression, come from communities of biological control agents on annual crops (e.g., Rosenheim et al., 1993) and/or predator communities dominated by predaceous arthropods (e.g., Finke and Denno, 2004). Thus it is perhaps surprising that the guild of predators considered here, predators and parasitoids attacking aphids on *B. oleracea* plants, appears to provide so little evidence of intraguild predation or other negative predator–predator interactions. Indeed, a long series of field experiments varying widely in design (Straub and Snyder, 2008; Snyder et al., 2006, 2008; Northfield et al., 2010; Gable et al., 2012), consistently shows complementarity among these predator species that strengthens herbivore suppression in multi-predator–species communities. We can suggest several possible reasons for this. First, several predator species in the *B. oleracea* community differ in where they forage on plants (Straub and Snyder, 2008; Gable et al., 2012), perhaps reducing the frequency of predator–predator contacts and thus opportunities for intraguild predation to occur (Schmitz, 2007). Second, this community lacks a generalist predator whose adult size greatly exceeds that of the other predator species, whereas such large size disparities have correlated with relatively high intraguild predation rates in several other systems (Ives et al., 2005). Finally, the parasitoid wasps that are often subject to intraguild predation when within the bodies of their hosts, appear able to “make up” for initial losses to intraguild predators through the wasps' relatively rapid reproduction and high fecundity (Snyder et al., 2006).

Ecologists interested in multi-predator effects have long debated the best way to manipulate predator species number. Additive designs, where the density of each predator species is held constant as more predator species are added, seek to ensure that intraspecific interference does not vary across species richness levels in order to measure the impacts of each species and the added benefit of pairing particular species. However, with these designs total predator density rises rapidly in highly-diverse treatments such that relatively few predator species can be considered at once. Substitutive manipulations avoid this problem by holding total predator densities constant across species-richness levels. However, they are generally unable to quantify both impacts of each species as well as additional benefits of particular species pairings. Furthermore, in both cases ecological realism is traded for the benefits of particular pairings within additive designs, or to separate the effects of species number from any confounding effect of total predator density in traditional substitutive designs (Naeem, 2008).

In some cases natural community assembly rules alter biodiversity effects by simultaneously altering species identity and richness, leading to stronger identity effects (Bracken et al., 2008), or altering the co-occurrence of complementary species (Zavaleta and Hulvey, 2004). Here, we suggest a hybrid approach, reproducing natural variation in predator species composition and relative abundance, and then using a generalized linear model to search for positive or negative interactions among each predator–species pairing. This approach allows predator communities to be varied across a natural gradient of species compositions, without sacrificing the ability to determine both predator species' individual impacts and their combined impacts when embedded in multi-predator assemblages. This approach allows for analyses analogous to those used in additive designs, but allows for greater variation in experimental treatments than those generally used in additive-designed experiments. In our experiment, we set total predator densities to the mean density observed in our open-field plots, according to a substitutive design. This allowed us to remove total predator density as an additional confounding variable, but carried as a cost a reduction in total density of each predator species as species richness increased. To add further realism, future experiments could use our analytical approach and also allow total predator density to vary, reflecting density differences seen across natural communities. Such an experiment would likely require a large number of experimental replicates and would still be subject to the cage effects inherent in many manipulative experiments, but where logistically feasible could shed valuable further insight into how multi-predator–species effects operate in nature.

We exploited natural variation in predator communities to determine whether multi-predator effects tended to generally improve or weaken overall herbivore suppression. This approach allowed us to use analyses similar to those used in additive designed experiments, while using a substitutive design that allowed greater variation in species richness. We found primarily positive multi-predator effects which strengthened prey suppression; some predator species declined in the presence of other predators but these effects were apparently too weak to impact overall aphid suppression. Our approach suggests a means to search for multi-predator effects across predator communities that is less influenced by experimental artifacts or limitations that emerge from particular experimental designs.

## 5. Declaration of authorship

T.D.N., D.W.C. and W.E.S. designed the experiment, T.D.N. and T.T. conducted the experiment, T.D.N. and D.W.C. analyzed the data with input from W.E.S., and T.D.N. and W.E.S. wrote the manuscript with input from D.W.C. and T.T.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2014.07.008>.

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