

TROPHIC AND GUILD INTERACTIONS  
IN BIOLOGICAL CONTROL

# Progress in Biological Control

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# Trophic and Guild Interactions in Biological Control

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Cover illustration:

Example of intra-guild competition. A female *Trichogramma turkestanica* parasitizes eggs of *Ephestia kuehniella* (top picture) and a larva of *Harmonia axyridis* predate both unparasitized (white) and parasitized (black) eggs of *Ephestia kuehniella* (bottom picture).

Pictures by D. Thibodeau and G. Boivin, Agriculture and Agri-Food Canada.

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## Preface

This book originates from a symposium we organized in May 2005 at a joint meeting of the Biocontrol Network of Canada and the International Organization for Biological Control in Magog, Québec, Canada. During this symposium, we discussed concepts of direct and indirect interactions among natural enemies of herbivores in natural and agricultural ecosystems — a field of growing interest in ecology and biological control.

Natural enemies of herbivores exist in nature as an assemblage of species that interact with one another and may transcend trophic levels. The community embracing a natural enemy can be complex and includes taxonomically dissimilar species of pathogens, parasitoids, and predators. These interactions involve predation and competition processes and share the typical characteristics of resource-consumer relationships where the resource species is killed and consumed by the other. Although they are mostly viewed as primary carnivores (developing on herbivores), natural enemies can also be secondary carnivores (when they attack other natural enemies), hosts, prey, or even herbivores, as several species may also feed on and acquire energy from plant resources.

Historically, research on biological control has been conducted using a vertical approach, focusing on simple trophic interactions between plants, herbivores and natural enemies. In the 1980s, this approach has been extended to multitrophic interactions to include contributions of the fourth trophic level. More recently, organisms that live below ground and may interact with higher trophic levels have been added to our knowledge. This trophic approach has been very successful as we now have a much better understanding of the role of bottom-up and top-down effects in both natural and managed ecosystems.

Guild interactions occur among species within the same trophic level. For example, complex relationships might evolve between a fungus, a parasitoid and a predator that exploit a herbivore. In our opinion, a key paper published in 1995 by Jay Rosenheim and his colleagues from the University of California, Davis has largely contributed to change our perception of the importance of guild interactions in biological control (Rosenheim, J.A., H.K. Kaya, L.E. Ehler, J.J. Marois and B.A. Jaffee, 1995. Intraguild predation among biological control agents: theory and evidence. *Biological Control* 5: 303-335). They concluded that intraguild interactions are widespread within communities of biological control agents of arthropod pests and that they are likely to influence the efficacy of biological control. The publication of this review has immediately stimulated original research on the nature and outcome of interactions among natural enemies. The literature is now filled with fascinating evidence of positive, negative, or neutral interactions between different types of biocontrol agents.

The study of trophic and guild interactions has led to a reconsideration of many paradigms in ecology, such as community structure, species exclusion, trophic

cascades in food webs, management of endangered species and biological control. From an applied perspective in biological control, understanding trophic and guild interactions is important to determine (i) the number and composition of species to release, (ii) the most suitable developmental stages of arthropods (or doses of pathogens) to be used, (iii) the timing of multiple species releases, and (iv) the impact of biological control agents on non-target species.

This book explores a broad range of ecological and evolutionary issues in animal species interactions, mostly in the context of biological control. From the beginning of this project we were seeking original viewpoints on a growing field. All authors have used ecological theory to better interpret emerging patterns of interactions in biological control. The core of the book is a series of chapters that examine how species interactions, such as competition, predation, parasitism, disease, mutualism, and omnivory affect population dynamics of natural enemies. Chapters include critical discussions of the current status of research in the field, comparative and meta-analyses, case studies, new data, models, and approaches to measure trophic and guild interactions. Drawing on a diversity of plant, herbivore and natural enemy examples from different ecosystems, each contribution illustrates how trophic and guild interactions, whether they be direct or indirect, simple or complex, strongly affect the efficiency of natural enemies and, over time, determine the outcome of biological control. The contributing authors were selected because they have each added significantly to our understanding of trophic and guild interactions in biological control. This book constitutes a survey of their knowledge, fresh perspective, efforts and enthusiasm.

We are therefore indebted to all authors for their dedication to the symposium and the book, including their help in reviewing chapters. Our deepest gratitude goes to Claude Godin for editorial assistance, compilation of the index and careful attention to detail throughout the book's production. We extend our appreciation to Zuzana Bernhart and Ineke Ravesloot, our editors at Springer, and to Heikki Hokkanen, editor of the book series 'Progress in Biological Control' for their helpful guidance in the production of this book. Finally, we wish to acknowledge the generous contributions of the Biocontrol Network of Canada and the International Organization for Biological Control towards the organization of the symposium and the publication of the book. In particular, these projects have required the coordinated efforts and encouragement of Raynald Laprade, Jean-Louis Schwartz, Robert Wiedenmann, Lucie Lévesque and Stéphane Dupont.

*Jacques Brodeur and Guy Boivin*

# THE INFLUENCE OF INTRAGUILD PREDATION ON THE SUPPRESSION OF A SHARED PREY POPULATION: AN EMPIRICAL REASSESSMENT

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**Abstract.** The experimental literature on the effects of intraguild predation on population growth rates of herbivorous arthropod prey has expanded substantially in the last decade, creating a body of results that can be used to test hypotheses relevant to biological control. Here we present a formal meta-analysis of the published experimental literature to assess two hypotheses: (1) intraguild predation causes an increase in the density of the shared herbivore prey, and (2) 'coincidental intraguild predation', in which a predatory arthropod (the 'intraguild predator') consumes a herbivore that harbors a developing parasitoid (the 'intermediate predator'), is less likely to disrupt biological control than is 'omnivorous intraguild predation', in which the intermediate predator is consumed directly. The meta-analysis reveals that intraguild predation does not universally cause an increase in the density of the shared prey; instead, the mean effect size viewed across all studies is not significantly different from zero, and there is strong variability in effects across studies. The meta-analysis also reveals a marginally significant difference between the effects of coincidental and omnivorous intraguild predation: inclusion of a coincidental intraguild predator significantly enhances biological control, at least in the short-term trials included in our database, whereas inclusion of an omnivorous intraguild predator has little overall effect. Thus, our analysis highlights the diversity of effects generated by intraguild predators within arthropod communities. The discrepancy between theory and empirics appears likely to stem from their different time-frames, with theory often emphasizing equilibria and experimentation examining instead short-term transients, and also with the artificial simplification of arthropod communities depicted in theoretical treatments. More work, both theoretical and empirical, is needed to bridge the gap between theory and observation and to develop a deeper understanding of factors generating the observed diversity of intraguild predator effects.

## 1. INTRODUCTION

The last fifteen years have witnessed a revolution in our understanding of the trophic structure of animal communities. From a view that emphasized functionally discrete trophic levels, as most forcefully enunciated by Hairston *et al.* (1960; see also Hairston and Hairston 1993, 1997), we have now moved to a new understanding of animal communities as often being replete with omnivory, defined as feeding at a variety of trophic levels (Hurd and Eisenberg 1990, Polis 1991, Wise 1993, Polis and Strong 1996, McCann *et al.* 1998, Rosenheim 1998, Halaj and Wise 2001, Finke and Denno 2004). For arthropod communities, two types of omnivory have been especially highlighted. First, many arthropods feed both as herbivores and as predators (Coll and Guershon 2002; see also Gillespie and Roitberg, this volume).

Second, many predatory arthropods feed on prey that are found at diverse locations within the food web, including insects that are detritivores, herbivores, and other predators (Polis *et al.* 1989, Rosenheim *et al.* 1995).

Intraguild predation is a type of omnivory that may have particular relevance to the suppression of herbivorous insects by their natural enemies. It occurs when two consumers that share a resource, and which therefore are potential competitors, also engage in predator-prey interactions with each other (Polis *et al.* 1989, Arim and Marquet 2004). Intraguild predation appears to be widespread in communities of biological control agents (Rosenheim *et al.* 1995, Sunderland *et al.* 1997, Janssen *et al.* 1998, Brodeur and Rosenheim 2000, Snyder *et al.* 2005).

The late Gary Polis and his colleagues produced a series of seminal papers that shaped both our theoretical and empirical understanding of intraguild predation (Polis *et al.* 1989, Polis 1991, Polis and Holt 1992, Polis and Strong 1996, Holt and Polis 1997). Although Polis himself did not work in applied insect ecology, he recognized the implications of his work for biological control, and he introduced the idea that intraguild predation might cause biological control programs to fail (Polis and Holt 1992). This idea was bolstered by two types of evidence. The first was a series of analytical models of a three-species module of interacting species: an intraguild predator, an intermediate predator, and a shared prey (which we will henceforth call the “herbivore”) (Polis *et al.* 1989, Polis and Holt 1992, Holt and Polis 1997). A salient prediction emanating from these models was that the presence of the intraguild predator increased the equilibrium density of the shared herbivore prey. The logic underlying this prediction was simple and compelling: in the simplest three-species module of intraguild predation, the two predators are in ‘perfect’ competition for the one species of prey that they both consume (the herbivore). Were there no direct trophic interactions occurring between the two predators (i.e., if they were only competitors and not engaged in intraguild predation), only one of the predators, the superior competitor, would be able to persist at equilibrium, while the inferior competitor would be competitively excluded. Theory demonstrates that the superior predator is the one that can sustain its population at the lowest equilibrium density of the herbivore prey population; that is, the superior competitor is always the best biological control agent. This is, of course, a happy outcome for biological control, because it means that the community would ‘self select’ the predator that produces the best pest control.

If, however, the two predators are not only competitors, but also engage in trophic interactions with one another, the outcome is quite different. The only way to achieve a stable three-species equilibrium is for the intraguild predator’s special advantage (it’s ability to consume the intermediate predator) to be balanced against some advantage possessed by the intermediate predator; the only possible advantage that the intermediate predator can have is a superior competitive ability. That is, the intermediate predator when present singly must be a better biological control agent than is the intraguild predator when present singly. In this case, for the intraguild predator to be present in a stable 3-species equilibrium, it must always elevate the

equilibrium density of the herbivore, because it suppresses the population of the superior biological control agent: the intermediate predator. This, of course, is an unhappy outcome for biological control.

Polis and Holt's earliest models have been extended in a variety of ways, to include variable ecosystem productivity, stage structure, saturating functional responses, and immigration (Diehl and Feissel 2000, Mylius *et al.* 2001, Revilla 2002, Briggs and Borer 2005, Ives *et al.* 2005). Most of these elaborations of the basic theory have upheld the basic prediction that intraguild predators should elevate the density of the herbivore. However, as explored in more detail below (see Discussion), recent work by Briggs and Borer (2005) has begun to demonstrate scenarios that broaden the possible range of expected outcomes. Thus, although theoretical treatments of intraguild predation are the first and primary basis for the expectation that intraguild predation has a negative influence on biological control, ongoing theoretical developments are beginning to cast doubt on how robust this prediction really is.

The second reason to think that intraguild predation might be a problem for biological control came from some of the earliest experimental studies of multi-predator biological control systems, which demonstrated exactly this unwanted outcome (Hoy *et al.* 1972, Press *et al.* 1974, Spiller 1986). Some of these studies were discussed by Polis and Holt in their early reviews. There were, however, actually very few studies that had involved experimental manipulations of intraguild predators, and thus the literature provided only the scantiest basis for a critical assessment of the prediction that intraguild predation always disrupts biological control (see Janssen *et al.* this volume).

The literature was still too immature to provide a definitive test when Ehler (1995) and Rosenheim *et al.* (1995) attempted to review what was known about intraguild predators in biological control systems. Their reviews did, however, produce a second and more nuanced prediction regarding the differential impact of two types of intraguild predation. The first type, called 'coincidental' intraguild predation by Polis *et al.* (1989), occurs only when an intraguild predator and an intermediate predator both attack the same herbivore individual. Coincidental intraguild predation occurs most often when a predator (the 'intraguild predator') attacks a herbivore that has previously been attacked by a parasitoid (or a pathogen; see Thomas *et al.* this volume), and which therefore harbors a developing offspring of the parasitoid (the 'intermediate predator'). In this case, intraguild predation will impose mortality on the intermediate predator population that is often similar in magnitude to the mortality that it imposes on the herbivore population – the two will generally be linked (and they will be equal in cases where the predator does not distinguish between parasitized and unparasitized hosts). In contrast, the second type of intraguild predation, termed 'omnivorous' intraguild predation by Polis *et al.* (1989), occurs without joint attack on the herbivore. Instead, intraguild predation occurs when one predator encounters and consumes another predator. In this case, the intraguild predator may impose mortality on the intermediate predator that is

independent of any direct effects on the herbivore population – it is easier to decouple mortality that is being imposed on the intermediate predator population and the herbivore population. This simple verbal argument, supported only weakly by the earliest hints of patterns emerging from the empirical literature, led to the suggestion that coincidental intraguild predation would have less potential to disrupt biological control than would omnivorous intraguild predation.

The intraguild predation literature has expanded dramatically in the last decade, providing the first opportunity to produce a quantitative synthetic test of the effect of adding an intraguild predator to a system made up of an intermediate predator and its herbivore prey. Here we present a formal meta-analysis of the literature on intraguild predation among natural enemies of terrestrial herbivorous arthropods to address two questions: (1) Does intraguild predation consistently lead to an elevated density of the shared herbivore population? (2) Is coincidental intraguild predation less disruptive of biological control than omnivorous intraguild predation?

## 2. METHODS

### 2.1. Survey of studies

We attempted to conduct an exhaustive survey of the peer-reviewed literature published through May 2005 to construct a dataset for analysis. Our criteria for including a study in the dataset were as follows. (1) The interacting species must have been terrestrial arthropods, including at least one herbivore and two natural enemies. (2) The trophic interactions must have been demonstrated to include intraguild predation; that is, both of the predators must have been known to feed on the shared herbivore population, and one predator (the ‘intraguild predator’) must have been demonstrated to feed upon the other (the ‘intermediate predator’). In all cases the intraguild predation was exclusively or primarily unidirectional. (3) The study must have included at least two experimental treatments, applied through manipulation of the system by the investigator: a ‘control’, in which the herbivore was present with only the intermediate predator, and an ‘intraguild predator treatment’ that was identical to the ‘control’ treatment in all respects except for the inclusion of one or more species of intraguild predators, thus completing the 3-species module. (4) The experiment must have employed an additive design, in which the intermediate predator was maintained at a constant density in the treatments with and without the intraguild predator present, as opposed to a replacement series, in which the total number of predators is maintained constant as the number of predator species present is increased. The relative merits of these two designs have been extensively discussed in the literature (Connolly 1988, Jolliffe 2000, see Straub and Snyder this volume); whereas the replacement series design may be particularly appropriate for some aspects of the study of how predator diversity *per se* influences biological control (e.g., Snyder *et al.* 2005), it is inappropriate for testing the effect of adding an intraguild predator, because it

confounds an interspecific effect (the effect of adding the intraguild predator) with an intraspecific effect (the effect of halving the density of the intermediate predator). (5) The experimental organisms must have been studied in the setting where they are normally found: in the field for arthropods found in natural ecosystems or attacking crops grown outdoors; in greenhouses for arthropods associated with greenhouse-grown crops; and indoors for arthropods that are economically significant in stored products settings. (6) The studies must have provided measurements of herbivore population densities and a measure of variance across replicates. Using these criteria, we identified 25 published articles that contributed a total of 30 observations concerning the effect of adding an intraguild predator (Table 1). Often, the published articles did not report all the information that we needed for the meta-analysis. Thus, we wrote to the authors and solicited the needed data. We received extremely generous assistance from the contacted authors; thus, this study reflects the collective efforts of the community of ecologists studying intraguild predation, both in the conduct of the original work and in the preparation of the raw dataset. In the few cases where the original data files were no longer available, means and variance estimates were estimated digitally from published figures.

A key assumption underlying formal meta-analysis is that the observations included in the dataset are statistically independent. In some cases, meta-analyses are now being conducted using explicit phylogenetic hypotheses of the relationships among the taxa being studied (e.g., Verdú and Traveset 2005). However, our study concerned interactions in 3-species modules, and techniques have not yet been developed to correct for phylogenetic effects in this case. In choosing an approach for defining independent observations, we also wanted to consider a second major concern for meta-analysis: the tendency for non-significant results to remain unpublished, generating substantial biases in the published literature. We reasoned that studies that reported comparative assessments of more than a single intraguild predator, intermediate predator, or herbivore were more likely to produce an unbiased measure of the distribution of possible intraguild predator effects, because if at least one of the tested predators produced a significant effect it would support the publication of the entire study. Thus, we extracted multiple data points from a single study when the study measured more than one target herbivore (Lang 2003), when the study measured more than one intraguild predator (Rosenheim *et al.* 1993, Rosenheim 2001, Colfer *et al.* 2003), or when the study included two qualitatively different environmental contexts (short plants versus tall plants, Snyder and Ives 2001). In all other cases, including cases where there were multiple herbivore density treatments and in which multiple experiments were performed on the same 3-species module, results were averaged across the multiple observations to produce a single entry in our final dataset.

## 2.2 Meta-analysis

For each study, the magnitude of the effect of the intraguild predator on the density of the herbivore was measured as a ln-transformed response ratio:

$$\ln R = \ln \left( \frac{\bar{X}^E}{\bar{X}^C} \right) \quad (1)$$

where  $R$  is the response ratio,  $\bar{X}^E$  is the mean herbivore density in the presence of the intraguild predator, and  $\bar{X}^C$  is the mean herbivore density in the absence of the intraguild predator. Negative values for  $\ln R$  indicate that herbivore densities are decreased in the presence of the intraguild predator (improved biological control), whereas positive values indicate elevated herbivore densities in the presence of the intraguild predator (disrupted biological control). The variance of this response measure was calculated as:

$$v_{\ln R} = \frac{(s^E)^2}{N^E (\bar{X}^E)^2} + \frac{(s^C)^2}{N^C (\bar{X}^C)^2} \quad (2)$$

where  $s^E$  and  $s^C$  are the standard deviation for the treatments with and without the intraguild predator, respectively, and  $N^E$  and  $N^C$  are the respective sample sizes. Osenberg *et al.* (1999) have emphasized the importance of choosing a metric for effect size that is appropriate for the underlying dynamics of the system being studied. The response ratio used here is ideal for studying instantaneous rates of exponential population growth. However, it does not account for variation in the duration of different experiments, which can be a key source of variation for meta-analyses. Osenberg *et al.* (1999) suggest that the response ratio be divided by the duration of each experiment to eliminate this important source of variation. We explored this approach, but found it to have a perhaps unexpected and undesirable outcome. If experiments are comparable in all respects except for their durations, then we might expect longer-duration studies to report larger response ratios, simply because the populations subjected to different treatments have had more time to diverge. However, when we examined the relationship between the absolute value of the response ratio and the duration of the experiment, we did not observe this expected positive relationship; instead we found exactly the desired result that experimental duration was not correlated with effect size ( $r = 0.000$ ,  $N = 30$ ,  $P = 0.99$ ). When we divided the response ratio by the duration of each experiment, we obtained a non-significant but still undesirable trend towards a negative relationship between the duration of the experiment and the absolute value of the effect size ( $r = -0.29$ ,  $N = 30$ ,  $P = 0.12$ ). We reason that different researchers choose a duration for their experimentation that matches the underlying tempo of the system being



studied. While short experiments are appropriate for some arthropods that reproduce very rapidly (e.g., aphids and mites), longer experiments are appropriate for arthropods that reproduce more slowly (e.g., some Lepidoptera). Thus, we chose to retain the time-dependent measure of the response ratio for our analyses. We did, however, correct our response ratio measure for variable experiment duration in those cases where the same 3-species module was tested in multiple experiments, and where we then averaged the replicate response ratios to produce a single datum for inclusion in the meta-analysis.

For most of the studies, we used herbivore densities measured at the end of the trial to calculate the response ratio (often, this was the only measure taken by the original workers). In cases where herbivore densities were measured repeatedly as a time-series and in which the relative values of the control and intraguild predator treatments changed markedly over the course of the experiment, we used the arithmetic mean herbivore densities across the duration of the experiment to calculate the response ratio. Variance estimates for mean herbivore densities across the duration of the studies were calculated for us *de novo* from the raw data by the authors of the original studies.

The meta-analysis was conducted using the MetaWin2.0 statistical program (Rosenberg *et al.* 2000). After checking for the existence of significant heterogeneity among studies, we discarded the fixed-effect model (the fixed-effect model provides a test of the hypothesis that intraguild predators generated the same effect size across all studies included in the data set), and fitted only random-effect models, which assume that different studies are estimating different effect sizes. To test whether or not the overall dataset was consistent with the hypothesis that the presence of an intraguild predator elevates herbivore densities, we asked whether a bootstrapped 95% confidence interval, constructed by re-sampling the dataset 999 times, overlapped zero. We also examined the effect of a categorical variable coding the type of intraguild predation (coincidental versus omnivorous). In an approach directly analogous to a standard ANOVA, MetaWin2.0 partitions the total variance in effect sizes into variance explained by the categorical variable and the residual, error variance. The significance of the variance explained by the categorical variable can then be tested using either a parametric test, using the  $\chi^2$  distribution, or a more conservative non-parametric randomization test; here, we report both test results. We used a 1-tailed test to reflect our *a priori* hypothesis that coincidental intraguild predation would be less disruptive of biological control.

Table 1. The full dataset of studies included in the meta-analysis examining the influence of intraguild predation on the density of the shared herbivore prey.

Herbivore	Intermediate predator	Intraguild predator	Type of intraguild predation	Expt length (days)	Effect size	Effect variance	Study
<i>Plodia interpunctella</i>	<i>Bracon hebetor</i>	<i>Xylocoris flavipes</i>	coincid	28	0.594	0.215	Press <i>et al.</i> 1974
<i>Melanoplus sanguinipes</i>	<i>Blaesoxipha hunteri</i>	Asilidae spp.	omniv	13	0.301	0.00840	Rees and Onsager 1982
<i>Aphis gossypii</i>	<i>Chrysoperla carnea</i>	<i>Orius tristicolor</i>	omniv	8	-1.128	0.198	Rosenheim <i>et al.</i> 1993, Rosenheim 2001
<i>Aphis gossypii</i>	<i>Chrysoperla carnea</i>	<i>Geocoris</i> spp.	omniv	7.8	0.281	0.150	Rosenheim <i>et al.</i> 1993, Rosenheim 2001
<i>Aphis gossypii</i>	<i>Chrysoperla carnea</i>	<i>Nabis</i> spp.	omniv	7.8	0.641	0.113	Rosenheim <i>et al.</i> 1993, Rosenheim 2001
<i>Aphis gossypii</i>	<i>Chrysoperla carnea</i>	<i>Zelus renardii</i>	omniv	8.7	1.700	0.080	Rosenheim <i>et al.</i> 1993, Cisneros and Rosenheim 1997, Rosenheim 2001
<i>Dactynotus</i> sp.	<i>Aphidius floridaensis</i>	<i>Cycloneda sanguinea</i>	coincid	18	0.270	0.177	Ferguson and Stiling 1996
<i>Diuraphis noxia</i>	<i>Aphelinus asychis</i>	<i>Paecilomyces fumosoroseus</i>	omniv	13	-0.119	0.0298	Mesquita <i>et al.</i> 1997
<i>Aphis gossypii</i>	<i>Lysiphlebus testaceipes</i>	<i>Hippodamia convergens</i>	coincid	24	-8.268	0.353	Colfer and Rosenheim 2001

Table 1. continued

<i>Acyrtosiphon pisum</i>	<i>Aphidius ervi</i>	<i>Pterostichus melanarius</i>	coincid	15	-0.364	0.044	Snyder & Ives 2001 (short plants)
<i>Acyrtosiphon pisum</i>	<i>Aphidius ervi</i>	<i>Pterostichus melanarius</i>	coincid	17	0.371	0.049	Snyder & Ives 2001 (tall plants)
<i>Anasa tristis</i>	<i>Nabis</i> sp.	Lycosids	omniv	83.5	0.871	0.120	Snyder & Wise 2001
<i>Tetranychus urticae</i>	<i>Phytoseiulus persimilis</i>	<i>Orius laevigatus</i>	omniv	28.7	-0.144	0.0546	Venzon <i>et al.</i> 2001
<i>Trialeurodes vaporariorum</i>	<i>Macrolophus caliginosus</i>	<i>Dicyphus tamaninii</i>	omniv	4	-0.285	0.00358	Lucas and Alomar 2002
<i>Acyrtosiphon pisum</i>	<i>Aphidius ervi</i>	<i>Harmonia axyridis</i> and <i>Nabis</i> sp.	coincid	31	-1.374	0.131	Cardinale <i>et al.</i> 2003
<i>Tetranychus</i> spp.	<i>Galendromus occidentalis</i>	<i>Orius tristicolor</i>	omniv	7	-4.376	0.149	Colfer <i>et al.</i> 2003
<i>Tetranychus</i> spp.	<i>Galendromus occidentalis</i>	<i>Geocoris</i> spp.	omniv	7	-0.528	0.130	Colfer <i>et al.</i> 2003
<i>Prokelisia</i>	<i>Tyrtus vagus</i>	<i>Pardosa littoralis</i>	omniv	38	0.897	0.120	Finke and Denno 2003
Aphids	Lycosids and Linyphiids	Carabids	omniv	37	0.0274	0.0539	Lang 2003
Thysanoptera	Lycosids and Linyphiids	Carabids	omniv	37	-0.332	0.0409	Lang 2003

Table 1. continued

Herbivore	Intermediate predator	Intraguild predator	Type of intraguild predation	Expt length (days)	Effect size	Effect variance	Study
Cicadellidae & Delphacidae	Lycosids and Linyphiids	Carabids	omniv	37	-0.0953	0.0473	Lang 2003
<i>Sitobion avenae</i>	Aphidiidae	Ground-dwelling predators	coincid	61	-0.165	0.0318	Schmidt <i>et al.</i> 2003
<i>Acyrtosiphon pisum</i>	<i>Aphidius ervi</i>	Generalist predators	coincid	21	-1.378	0.166	Snyder and Ives 2003
<i>Prokelisia</i>	<i>Grammonota trivittata</i>	<i>Pardosa littoralis</i>	omniv	49	-1.025	0.339	Denno <i>et al.</i> 2004
<i>Plutella xylostella</i>	<i>Cotesia plutellae</i> and others	<i>Solenopsis invicta</i>	coincid	70.5	-0.092	0.0635	Harvey & Eubanks 2004
<i>Tetranychus cinnabarinus</i>	<i>Phytoseiulus macropilis</i>	<i>Nesticodes rufipes</i>	omniv	11.5	-0.102	0.0444	Rosenheim <i>et al.</i> 2004a
<i>Tetranychus cinnabarinus</i>	<i>Stethorus siphonulus</i>	<i>Nesticodes rufipes</i>	omniv	10.33	0.545	0.0532	Rosenheim <i>et al.</i> 2004b
<i>Macrosiphum euphorbiae</i>	<i>Aphelinus asychis</i>	<i>Harmonia axyridis</i>	coincid	45	-0.593	0.114	Snyder <i>et al.</i> 2004
<i>Trialeurodes vaporariorum</i>	<i>Encarsia formosa</i>	<i>Dicyphus hesperus</i>	coincid	19	-0.0294	0.1150	McGregor & Gillespie 2005
<i>Musca domestica</i>	Small carabids	<i>Pterostichus melanarius</i>	omniv	7	0.051	0.384	Prasad and Snyder in press

### 3. RESULTS

#### 3.1. Effects of intraguild predation on herbivore density

The overall effect of moving from a 2-species module (herbivore + intermediate predator) to a 3-species module (herbivore + intermediate predator + intraguild predator) was not as predicted by theory. Instead of producing a significant increase in herbivore densities, the mean effect size was  $-0.38$ , with a bootstrapped 95% confidence interval that overlapped zero (Fig. 1). Thus, across all the studies, adding an intraguild predator had no significant effect on herbivore densities, with a non-significant trend towards a slight improvement of biological control (the  $-0.38$  value represents a 31% decrease in herbivore densities when the intraguild predator is present).

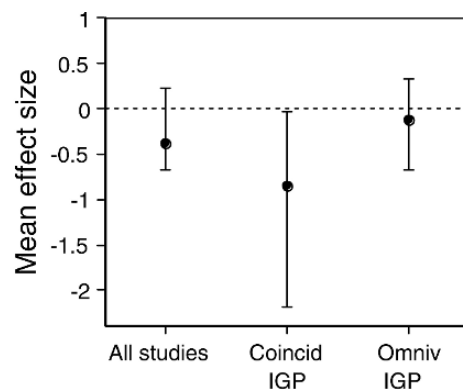


Figure 1. Mean influence of intraguild predation on the density of the shared herbivore population, measured as  $\ln(\bar{X}^E / \bar{X}^C)$ , observed across all studies in the meta-analysis. Shown are the means and bootstrapped 95% confidence intervals for all studies ( $N = 30$ ), for studies of coincidental intraguild predation (Coincid IGP;  $n = 11$ ), and for omnivorous intraguild predation (Omniv IGP;  $n = 19$ ). Negative values indicate that the presence of the intraguild predator results in a decrease in herbivore density.

There was significant heterogeneity across the 30 studies in the magnitude of the effect size ( $Q_T = 100.3$ ,  $df = 29$ ,  $P < 0.00001$ ). Thus, although the overall mean was not significantly different from zero, the variance among effect sizes was greater than expected simply by sampling error. This suggests that different systems exhibit significantly different outcomes: in some cases, adding an intraguild predator elevates herbivore density, and in other cases it depresses herbivore density. This result was reinforced by the observation that at least in some cases, the response ratios observed in replicate observations of a given 3-species module were repeatable. For example, the meta-analysis included a single datum for the 3-species

module of *Aphis gossypii* (Aphididae) (herbivore), *Chrysoperla carnea* (Chrysopidae) (intermediate predator), and *Zelus renardii* (Reduviidae) (intraguild predator), which represented the mean of five independent experimental trials; the trials produced quite concordant response ratio measures (1.93, 1.35, 1.71, 1.71, 1.83). The distribution of effect sizes included many studies that produced only small effects on herbivore densities, some studies that produced large increases in herbivore densities, and other studies that produced dramatic decreases in herbivore densities (Fig. 2). The meta-analysis therefore allows us to reject emphatically the notion that intraguild predation produces one consistent type of effect on herbivore densities. Variability is instead the dominant result.

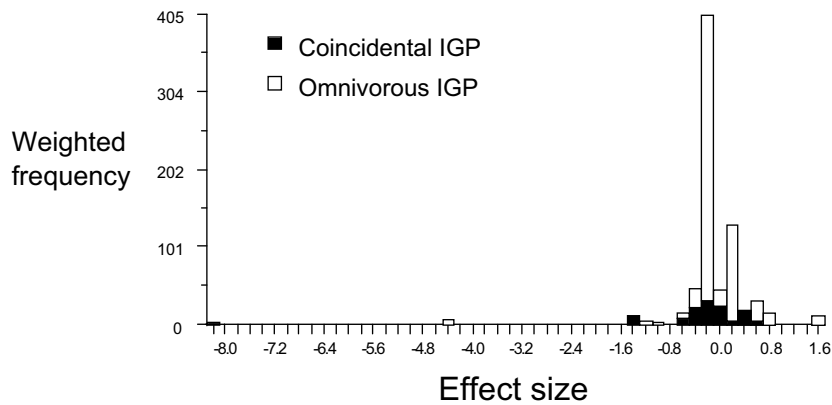


Figure 2. Distribution of effect sizes of intraguild predation on the density of the shared herbivore population observed for coincidental and omnivorous intraguild predation. Effect sizes are measured as  $\ln(\bar{X}^E / \bar{X}^C)$ ; thus positive values indicate that the intraguild predator elevated herbivore density, and negative values indicate that the intraguild predator suppressed herbivore density. The vertical axis shows the weighted frequency (weights =  $1/\text{variance}$ ), and thus the histogram shows the relative contribution of the data to each effect class (coincidental versus omnivorous intraguild predation) rather than the sample size for that effect class.

### 3.2. Coincidental versus omnivorous intraguild predation

Eleven of the 30 observations in the dataset involved coincidental intraguild predation, where predators attacked parasitized herbivore prey, thereby consuming both the herbivore and the developing parasitoid (the intermediate predator), with the remaining 19 cases examples of omnivorous intraguild predation. The analyses provided only mixed support for the hypothesis that coincidental intraguild predators were less likely to elevate herbivore densities than were omnivorous intraguild predators: the less conservative parametric test was significant ( $Q = 4.4$ ,  $df = 1$ ,  $P = 0.018$ ), whereas the more conservative randomization test was not ( $P = 0.12$ ). The

significance of the parametric test was lost if (a) the analysis was conducted without weighting the observations by their associated variance estimates ( $Q = 1.6$ ,  $df = 1$ ,  $P = 0.10$ ) or (b) the strongest outlier (Colfer and Rosenheim 2001) was excluded ( $Q = 1.5$ ,  $df = 1$ ,  $P = 0.11$ ). The mean effect size for coincidental intraguild predation was  $-0.84$  (a 57% decrease in herbivore density), and the bootstrapped confidence interval did not overlap zero (Fig. 1). Thus, our analysis suggests that adding a coincidental intraguild predator to a herbivore/intermediate predator system results in an overall improvement in herbivore suppression, at least in the short-term trials included in our data set. In contrast, the mean effect size for omnivorous intraguild predation was close to zero (mean effect size =  $-0.12$ ); these studies included cases of predators eating other predators, predators eating adult parasitoids, and a pathogen infecting an adult parasitoid (Table 1). Our analysis provides the first empirical support for the idea that coincidental intraguild predation has a reduced potential to disrupt biological control.

#### 4. DISCUSSION

##### *4.1. Intraguild predation and the density of the shared prey population*

The earliest and most influential models of intraguild predation predicted that intraguild predators increase the equilibrium density of the shared prey population (Polis *et al.* 1989, Polis and Holt 1992, Holt and Polis 1997). Translated into the context of applied insect ecology, this suggests that intraguild predators will always act to disrupt biological control, suppressing populations of intermediate predators and thereby allowing herbivore populations to expand. Nevertheless, our analysis of the experimental literature on intraguild predation in terrestrial arthropod communities does not support any single, dominant effect of intraguild predators. Instead, our primary result is that intraguild predators have widely variable effects on herbivore populations. Some intraguild predators produce dramatic decreases in herbivore populations, whereas others have the reverse effect, triggering herbivore outbreaks. Strikingly, the overall effect size, viewed across all studies, was not significantly different from zero.

How can we explain the discrepancy between the empirical record and the theoretical predictions? We suggest two primary possibilities. The first is that there is a profound disconnect between the time frames of the empirical and the theoretical work: while the theory has been almost universally concerned with long-term equilibrium conditions, the empirical work has been almost entirely very short-term (Venzon *et al.* 2001, Hastings 2004, Briggs and Borer 2005). Indeed, the mean duration of the experiments included in our dataset was a mere 25.5 days (range: 4–83.5 d). Even for arthropods, these are very short experiments, in at least some cases too short to incorporate reproductive recruitment of the intermediate and intraguild predators. As incisively demonstrated by Briggs and Borer (2005), short-term transient effects of intraguild predators may be very different from the long-term

equilibrium effects. As noted earlier, to achieve a stable 3-species equilibrium, the intraguild predator must be an inferior biological control agent of the herbivore population in comparison to the better competitor, the intermediate predator. In contrast, in a non-equilibrial setting, there is no reason to exclude the possibility that the intraguild predator has all the advantages over the intermediate predator – that is, it may be the best competitor (and therefore the best biological control agent) and also be able to exploit the intermediate predator as a food resource. In this case, it is not all surprising that adding the intraguild predator to the system would improve herbivore control.

This may be exactly the scenario that underlies some of the most dramatic cases of improved herbivore control following introduction of an intraguild predator. For example, *Geocoris* spp. (Hemiptera: Lygaeidae), *Orius tristicolor* (Anthocoridae), and *Galendromus occidentalis* (Phytoseiidae) are three important predators of herbivorous spider mites *Tetranychus* spp. (Tetranychidae) in cotton (Colfer *et al.* 2003). These predators engage in a size-structured ladder of intraguild predation, in which the larger species feed on progressively smaller species: so, *Geocoris* feeds on *Orius*, and both feed heavily on *Galendromus* (Rosenheim 2005). In at least some short-term trials, *Geocoris* and *Orius* are better at controlling spider mites than is *Galendromus* (R. G. Colfer, pers. comm.). The observation, then, that adding *Geocoris* or *Orius* to a 2-species module of *Galendromus* + spider mites produces strong improvements in biological control is not surprising (Colfer *et al.* 2003). Because *Geocoris* and *Orius* may be better short-term competitors and intraguild predators of *Galendromus*, they might be expected to exclude *Galendromus* from cotton. And, indeed, *Galendromus* does appear to be excluded from cotton by intraguild predation, even when their populations are augmented experimentally with large releases (Colfer *et al.* 2004). But, what does this tell us about the longer-term dynamics? Perhaps not much. Spider mites exhibit irruptive dynamics in cotton fields, even in organically-managed cotton fields that are not subject to pesticide-generated disruptions (unpubl. data). *Galendromus* may not be the best predator of spider mites in the shortest-term trials in cotton, but it has been demonstrated to be a highly effective long-term biological control agent in more stable perennial cropping systems (Nyrop *et al.* 1998), and even in longer-term cage trials in cotton it may outperform *Orius* and *Geocoris* (R. G. Colfer, pers. comm.). We do not know why, in the long term, *Geocoris* and *Orius* cannot control spider mite populations in cotton, but other natural enemies (predators, parasitoids, and pathogens) that suppress their populations are the leading candidate explanations (Rosenheim 2005). Thus, in this system, and probably in many others, short-term and long-term effects of interactions within communities of natural enemies may be very different indeed.

There is a second disconnect between the theory and the real setting of the empirical work: the theory has been developed for a closed 3-species module, with perfect competition between the intraguild predator and the intermediate predator for a single shared prey, whereas in nature most systems are open and predators have diverse prey resources. This is particularly true for intraguild predators. A predator



that has a diet broad enough to include a herbivore and another predator is very likely to consume multiple species of herbivore prey, and often plant-based resources as well (Arim and Marquet 2004). Holt and Polis (1997) suggested that their prediction that intraguild predators universally increase the density of the shared prey was likely to be sensitive to the addition of alternate prey. Our unpublished simulations have shown that this is the case: moving from a 3-species module to a 4-species module incorporating a second species of herbivore prey, immediately opens up the possibility that the lowest density of the target herbivore is achieved with both predators present in a 4-species equilibrium (unpubl. data). Briggs and Borer (2005) have also shown that immigration of the intraguild and intermediate predators, which can be thought of as another form of subsidy from an alternate resource, can have exactly this effect. While some intraguild predation systems may conform to the simplest 3-species configuration modelled by Holt and Polis, we suspect that most will not.

#### 4.2. *Coincidental versus omnivorous intraguild predation*

Our analysis has provided the first empirical support for the hypothesis that coincidental intraguild predation may have less potential to disrupt biological control than omnivorous intraguild predation. Why might this be? There is no published theoretical work comparing the dynamical significance of these two forms of intraguild predation, so we are left with verbal argumentation. We tentatively suggest the following line of reasoning. For both coincidental and omnivorous intraguild predation, a key determinant of overall implications for biological control is the intraguild predator's preference for consuming the intermediate predator versus the herbivore. We suggest that omnivorous intraguild predators may be more likely to exhibit a preference for consuming the intermediate predator than are coincidental omnivorous predators. Consider first an omnivorous intraguild predator, which chooses between two potential prey: an intermediate predator, which in this case is generally another freely-foraging predator, or an herbivore. These two prey types may often occupy different microhabitats on the plant, differ significantly in body size, and differ in foraging or defensive behavior. These differences create abundant opportunities for different encounter probabilities, willingness to initiate attacks, and likelihood of subduing a prey given an attack. Strong preferences for one type of prey over another can decouple the mortality imposed by the intraguild predator on the intermediate predator population from that imposed on the herbivore population. In many cases, the intermediate predator may be more mobile than the herbivore, and thus may be at greater risk of attack (Rosenheim *et al.* 2004b). Biological control may be disrupted when an omnivorous intraguild predator generates strong mortality of the intermediate predator population but minimal mortality of the herbivore population.

Consider now a coincidental intraguild predator, which chooses between two potential prey: an intermediate predator, which in this case is an immature parasitoid

developing within the herbivore, or the herbivore itself (now in an unparasitized state). We suggest that these two prey types are much more likely to occupy similar microhabitats, be similar in size, and be similar in behavior, because we are now simply comparing parasitized versus unparasitized individuals of the same species. Although the empirical record does show that predators may in some cases have strong preferences for consuming either parasitized (e.g., Jones 1987, Snyder and Ives 2001) or unparasitized individuals (e.g., Ruberson and Kring 1991), the most common result is that predators do not distinguish between parasitized and unparasitized individuals early during the parasitoid's development, and later develop an increasing preference for unparasitized hosts (reviewed in Rosenheim *et al.* 1995, Brodeur and Rosenheim 2000). Thus, in general, we expect coincidental intraguild predators to impose similar or somewhat lower levels of mortality on the intermediate predator population (the parasitoid) than on the herbivore population. Opportunities to release herbivores from control thus seem likely to be diminished.

#### 4.3. *Where do we do from here?*

Ecologists in search of broad generalizations are often disappointed at the end of the day. The view that all predators operate from the third trophic level, acting reliably to suppress populations of herbivores and thereby freeing plants from strong effects of herbivory (Hairston *et al.* 1960) is no longer tenable. Our synthesis of the experimental literature suggests that the view that all intraguild predators act to disrupt the control of their shared herbivore prey is equally untenable. Instead, different intraguild predators seem to have very different effects on herbivore population suppression, at least in the short term.

What sort of work is now most needed? We suggest two approaches. First, we need to bring the theory and the real world tests of theory closer together. This will require renewed work by both the empiricists and the theoreticians. Empiricists will need to overcome the logistical barriers to conducting longer-term experiments to observe the dynamics of intraguild predators, intermediate predators, and their prey over multiple generations. Whether empiricists working with arthropods will ever be able to run experiments long enough to observe real equilibria is open to question, but it seems both reasonable and important to include at least several generations of all the key players to reach conclusions about longer-term effects of intraguild predation. This may require careful choices about which systems to study. Theoreticians will need to devote additional attention to the transient effects of intraguild predators (e.g., Venzon *et al.* 2001, Snyder and Ives 2003) and build models with more realistic representations of the array of resources available to most predators in nature. Work on transient dynamics is important because many real world systems are inherently non-equilibrial; this is especially true for agroecosystems, where regular disturbances are the norm, and management decisions may hinge entirely on events occurring during a short growing season or a narrow window of crop vulnerability to herbivore damage.