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THE INFLUENCE OF INTRAGUILD PREDATION ON PREY SUPPRESSION AND PREY RELEASE: A META-ANALYSIS

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Abstract. Intraguild predation (IGP) occurs when one predator species consumes another predator species with whom it also competes for shared prey. One question of interest to ecologists is whether multiple predator species suppress prey populations more than a single predator species, and whether this result varies with the presence of IGP. We conducted a meta-analysis to examine this question, and others, regarding the effects of IGP on prey suppression. When predators can potentially consume one another (mutual IGP), prey suppression is greater in the presence of one predator species than in the presence of multiple predator species; however, this result was not found for assemblages with unidirectional or no IGP. With unidirectional IGP, intermediate predators were generally more effective than the top predator at suppressing the shared prey, in agreement with IGP theory. Adding a top predator to an assemblage generally caused prey to be released from predation, while adding an intermediate predator caused prey populations to be suppressed. However, the effects of adding a top or intermediate predator depended on the effectiveness of these predators when they were alone. Effects of IGP varied across different ecosystems (e.g., lentic, lotic, marine, terrestrial invertebrate, and terrestrial vertebrate), with the strongest patterns being driven by terrestrial invertebrates. Finally, although IGP theory is based on equilibrium conditions, data from short-term experiments can inform us about systems that are dominated by transient dynamics. Moreover, short-term experiments may be connected in some way to equilibrium models if the predator and prey densities used in experiments approximate the equilibrium densities in nature.

Key words: intraguild predation; lentic; log response ratio; lotic; meta-analysis; marine; multiple predator species; prey release; prey suppression; terrestrial invertebrates; terrestrial vertebrates.

INTRODUCTION

Intraguild predation (IGP) occurs when one predator species consumes another predator species with whom it also competes for shared prey (Polis et al. 1989, Holt and Polis 1997; see Plate 1). IGP can be unidirectional, with one species functioning as the top (i.e., intraguild) predator and the other functioning as the intermediate predator (i.e., intraguild prey), or mutual, where each predator has the ability to consume the other. Ecologists are often interested in knowing whether multiple predators lead to lower prey densities than the most effective single predator, especially in the context of biological control (Murdoch et al. 1985, Cory and Myers 2000, Cardinale et al. 2003). Multi-predator prey suppression occurs when prey density is lower with both predators present than with either predator alone, whereas prey release occurs if prey density is greater in the presence of both predators. IGP is often considered a factor that can release prey from predator control, but it does not necessarily do so.

Most intraguild predation theory is based on long-term equilibrium models (Holt and Polis 1997), whereas many experiments examining IGP document short-term, transient dynamics (Murdoch et al. 1985, Holt and Lawton 1993, Fenton et al. 2001, Briggs and Borer 2005). Equilibrium models suggest that for three-species intraguild predation assemblages to be stable, the intermediate predator must be more effective at consuming the shared prey than the top predator (Holt and Polis 1997). In such cases, the introduction of a top predator is predicted to weaken prey suppression by reducing the numbers and foraging activity of the intermediate (and more effective) predator. Although IGP is generally recognized to influence interactions between multiple predators (Rosenheim et al. 1993, Sih et al. 1998), the effects of adding a top predator on prey suppression are poorly understood. An improved understanding of IGP and multiple predator effects will

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facilitate predictions about the consequences of adding or removing species from a community (e.g., in the context of biological control or conservation).

Published experimental studies provide us with examples of both prey suppression and prey release with multiple predators, and it is not well understood why prey differ in their response to multiple predator species. However, some hypotheses can be suggested. Adding a top predator to an assemblage comprising an intermediate predator and shared prey can generate two opposing effects: (1) it introduces a consumer that imposes mortality on the shared prey (a direct, negative effect), and (2) it introduces a source of mortality and fear for the intermediate predator, thus generating an indirect, positive effect on the shared prey. The relative magnitudes of these two opposing effects are likely to depend, at least in part, on how effective the top and intermediate predators are as direct consumers of the shared prey. Thus, we predict that the occurrence and magnitude of prey suppression vs. prey release will depend on the relative ability of the two predator species to suppress the shared prey.

We also expect that the ecosystem (i.e., lotic, agricultural field) in which the interactions occur may be important because food webs in aquatic ecosystems have been suggested to be more linear than those in terrestrial ecosystems (Strong 1992), with fewer species to dampen the influence of top predators (Polis 1991). A comparative analysis of trophic cascade strengths also found that predator effects vary considerably across different ecosystems (Shurin et al. 2002).

In the past 10 years, many papers have been published that examine intraguild predation. We used this large body of existing information to examine the influence of intraguild predation on the detection of prey suppression vs. prey release. Using meta-analysis, we address the questions: (1) Does the presence of mutual or unidirectional IGP affect the relative ability of pairs of predators to suppress prey in comparison to single predator species? (2) In assemblages with unidirectional IGP, is the intermediate predator more effective than the top predator at suppressing prey populations when alone? (3) Does the addition of a top predator vs. an intermediate predator have a consistently different effect on the density of shared prey? (4) Does the effect of adding a top or intermediate predator depend on the effectiveness of each predator when alone? and (5) Do ecosystems (i.e., lotic, lentic, marine, terrestrial invertebrates, terrestrial vertebrates) differ in their responses (suppression or release) to multiple predator species?

METHODS

We compared the effects of intraguild predation using meta-analysis to examine general patterns across studies (Gurevitch and Hedges 1999, Osenberg et al. 1999). We searched an electronic database, Web of Science, and citations within papers on the database for studies that included at least two predator species and a shared prey. We included papers that provided the following information: final number of prey in treatments with each predator alone, final number of prey in the presence of both predator species, final number of prey in a no predator control, and an estimate of variance for each of these numbers. In some cases, data not available in the publication were obtained from the original authors. Data were used to obtain effect sizes and variances (see *Effect sizes: prey suppression vs. prey release*). We also used information from these papers and other sources to determine if the two predators were able to feed on one another. Studies were categorized by ecosystem: lotic, lentic, marine, terrestrial invertebrates, and terrestrial vertebrates.

To retain statistical independence in the data, we averaged some effect sizes and variances. For example, many papers reported multiple studies (e.g., a study of two predators and a prey under two different environmental conditions) and others provided data at multiple times for a single study. We calculated the effect sizes (see below) and variances for each study or time separately. For the studies that involved multiple measurements through time, multiple prey or predator densities, or the same experiment repeated in multiple years, we then averaged the effect sizes (and variances) to arrive at a single effect size (and variance). For papers that included multiple studies that varied levels of heterogeneity, experimental location, predator or prey species, temperature, or life stages, all effect sizes were retained.

Effect sizes: prey suppression vs. prey release

We tested the prediction that prey suppression would be weakened in the presence of multiple predator assemblages (compared to single predator assemblages) by quantifying relative suppression effectiveness (R_S):

$$R_S = \ln\left[\frac{\min(N_1, N_2)}{N_{\mathrm{Both}}}\right] \qquad (1)$$

where N_1, N_2, and N_{Both} are the final number of shared prey in treatments with predator 1, predator 2, and both predators together, respectively. This effect size is a log response ratio, which is commonly used in ecological meta-analyses (Osenberg et al. 1997, Borer et al. 2005) and has well understood statistical properties (Hedges et al. 1999). $R_S = 0$ represents equal suppression of the shared prey by the most effective single predator alone and by the multiple predator assemblage. $R_S > 0$ represents the situation in which a multiple predator assemblage suppresses the prey more than the most effective single predator when alone, and $R_S < 0$ represents the situation in which the most effective single predator alone suppresses the prey more than the multiple predator assemblage. Effect sizes were calculated for assemblages not believed to have IGP, and those species groupings in which unidirectional or mutual IGP was thought to potentially occur. The variance of all log ratios was calculated as follows:

$$V = \left[\frac{(\sigma_x)^2}{(N_x)^2}\right] + \left[\frac{(\sigma_y)^2}{(N_y)^2}\right] \quad (2)$$

where σ_x and σ_y are the standard errors for the effect size numerator (e.g., mean final number of prey in treatments with the most effective single predator only) and the effect size denominator (e.g., both predators), respectively. N_x and N_y are the final number of prey in the effect size numerator (e.g., mean final number of prey in treatments with the most effective single predator only) and the effect size denominator (e.g., both predators), respectively.

For the remaining effect size calculations, we only included studies in which unidirectional IGP was documented to occur. To test the prediction based on IGP theory that the intermediate predator alone should be more effective than the top predator alone at suppressing the shared prey, we quantified relative predator effectiveness (R_E):

$$R_E = \ln\left(\frac{N_{IP}}{N_{TP}}\right) \quad (3)$$

where N_{IP} and N_{TP} are the final number of shared prey in treatments with the intermediate predator only, and the top predator only, respectively. The interpretation of R_E is directly analogous to that for R_S. The variance of R_E, V_{R_E}, was calculated using Eq. 2.

The magnitude of the effect of adding a top predator to the assemblage on the density of the shared prey (E_{TP}) was measured as

$$E_{TP} = \ln\left(\frac{N_{IP}}{N_{Both}}\right). \quad (4)$$

$E_{TP} = 0$ indicates no effect of adding the top predator (relative to the intermediate predator alone). $E_{TP} < 0$ represents situations in which adding the top predator releases prey because the intermediate predator alone suppresses the shared prey more than the combined predator treatment, and $E_{TP} > 0$ represents situations in which adding the top predator causes increased prey suppression. The variance of E_{TP}, V_{E_TP}, was calculated using Eq. 2.

The effect of adding an intermediate predator to the assemblage on the density of the shared prey (E_{IP}) in assemblages with IGP was calculated as

$$E_{IP} = \ln\left(\frac{N_{TP}}{N_{Both}}\right) \quad (5)$$

where the interpretation of E_{IP} is directly analogous to that for E_{TP}. The variance of E_{IP}, V_{E_IP}, was calculated using Eq. 2.

Finally, we calculated relative suppression of the shared prey with the intermediate predator and top predator alone as follows:

$$S_{IP} = \ln\left(\frac{N_{IP}}{N_{Control}}\right) \quad (6)$$

$$S_{TP} = \ln\left(\frac{N_{TP}}{N_{Control}}\right). \quad (7)$$

Statistical analysis

We used MetaWin 2.1 (Rosenberg et al. 2000) and random effects models for summary analyses for groups of studies. Comparisons among groups of studies were made using a mixed model, which partitions total variance into variance explained by the categorical variable, variance among studies (within categories), and the within-study variance extracted from the primary article. The significance of the variance explained by the categorical variable was evaluated with a non-parametric randomization test. We resampled the data set 999 times and examined whether the resulting bootstrapped 95% confidence intervals overlapped zero and whether the confidence intervals for each comparison overlapped. Most analyses were conducted for all data together ("all ecosystems" in figures) and for each ecosystem separately (i.e., lotic, lentic, marine, terrestrial invertebrates, and terrestrial vertebrates).

We determined whether prey suppression was weakened in multiple predator assemblages due to the possibility of unidirectional and/or mutual IGP (i.e., relative suppression effectiveness; Eq. 1). In assemblages where unidirectional IGP was known to occur, we determined whether the top predator or intermediate predator was more effective at suppressing the shared prey when alone (i.e., relative predator effectiveness; Eq. 3), and whether this varied by ecosystem. We also determined whether prey suppression or prey release occurred as a consequence of adding a top predator (i.e., E_{TP}; Eq. 4) or an intermediate predator (i.e., E_{IP}; Eq. 5), and whether this varied by ecosystem. Finally, we used SYSTAT (SYSTAT Software 2004) to conduct unweighted regression analysis to examine the relationship between adding a top or intermediate predator to an assemblage and relative suppression with the intermediate predator (S_{IP}, Eq. 6) or top predator (S_{TP}; Eq. 7) alone. To avoid potential spurious correlations in the comparisons in which the same term appeared in the x and y variable in these regressions, we used Monte Carlo simulations (using Matlab; The MathWorks, Natick, Massachusetts, USA) in which the sequence of N_{IP} or N_{TP} and N_{Both} randomly shifted. We then calculated new E_{IP}, E_{TP}, S_{IP}, and S_{TP} values in which the numerators and denominators had been shuffled, and ran a regression between the "new" x and y pair to find the slope estimate. We repeated this process to obtain 1000 slope estimates. We determined the critical values marking the top and the bottom 2.5% and compared our slope estimates from SYSTAT to those values. If our actual slope estimate was more extreme than the critical values marking the 2.5% tails of the null distribution, we considered our results to be significant (Dean and Cao 2003).

We used unweighted regression analyses in SYSTAT to examine the relationships between the magnitude of

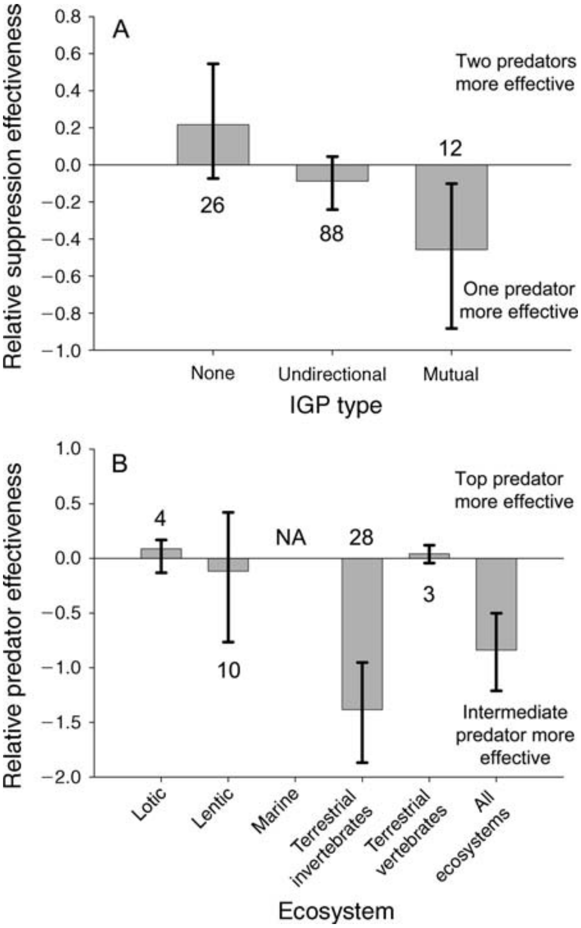

FIG. 1. (A) Relative suppression effectiveness (R_S) for assemblages with one vs. two predator species. R_S (Eq. 1) is a measure of the effectiveness of the more effective single predator species relative to both predator species together at suppressing the shared prey. Positive values indicate that two predators together are more effective, whereas negative values indicate that single predator species are more effective at suppressing the shared prey. (B) Relative predator effectiveness (R_E) for assemblages with unidirectional IGP. R_E (Eq. 3) is a measure of the relative effectiveness of the top and intermediate predators alone at suppressing the shared prey. Positive values indicate that the top predator is more effective, whereas negative values indicate that the intermediate predator is more effective at suppressing the shared prey. All values are means ± bootstrapped 95% CI. The number above or below each bar gives the number of studies used to calculate the mean. NA designates cases in which the sample size was less than two.

the resulting effect sizes and (1) the length of each experiment and (2) the area of the experimental venue.

RESULTS

The database used for these analyses included 56 papers making 126 comparisons (26 lentic, 31 lotic, eight marine, 58 terrestrial invertebrate, and three terrestrial ecosystems in which at least one species was a vertebrate; see the Appendices and Supplement for more information). The type of IGP thought to occur in an assemblage influenced the relative effectiveness of multiple predator assemblages vs. single predator assemblages at suppressing the shared prey (relative suppression effectiveness; $P = 0.019$; Fig. 1A). Specifically, as the number of trophic linkages between the two predators (0 = no IGP, 1 = unidirectional IGP, 2 = mutual IGP) increased, the likelihood of prey release in the presence of multiple predator species increased (no IGP, mean = 0.2173, CI = −0.0736 to 0.5457; unidirectional IGP, mean = −0.0877, CI = −0.2412 to 0.0442; mutual IGP, mean = −0.4578, CI = −0.8836 to −0.1012).

As predicted by theory, when all ecosystems were combined the intermediate predator was more effective than the top predator at suppressing the shared prey when alone (mean relative predator effectiveness = −0.8385, CI = −1.2109 to −0.5012). This effect was largely due, however, to data from terrestrial invertebrate ecosystems (Fig. 1B). Ecosystems differed significantly ($P = 0.009$) in the relative effects of intermediate vs. top predators. In ecosystems other than terrestrial invertebrates, intermediate and top predators were equally effective at suppressing the shared prey.

For all ecosystems combined, adding a top predator to an assemblage that already had an intermediate predator caused prey to be released (mean = −0.2750, CI = −0.6244 to 0.0069; Fig. 2A), whereas adding an intermediate predator to an assemblage that already had a top predator had the reverse effect, suppressing prey (mean = 0.4057, CI = 0.2547 to 0.5691; Fig. 2B). Thus, adding a top predator increased prey density, and adding an intermediate predator decreased prey density. However, this result was primarily due to responses observed in terrestrial invertebrate ecosystems (the ecosystem for which we had the most data); ecosystems differed significantly in the effect of adding a top predator ($P = 0.039$), but not an intermediate predator ($P = 0.356$). Adding a top predator tended to release prey in terrestrial invertebrate ecosystems, whereas lotic and terrestrial vertebrate ecosystems tended to show prey suppression with the addition of a top predator. Only terrestrial invertebrate ecosystems showed a difference in the effect of adding an intermediate vs. a top predator.

The effects of adding a top predator depended on the effectiveness of the top and especially the intermediate predators when they were alone. When intermediate predators alone were particularly effective at suppressing prey, adding the top predator caused a strong prey release (Fig. 3A), presumably because the top predator caused a reduction in the density (or feeding rate) of the effective intermediate predator. This pattern was apparent for both lentic and terrestrial invertebrate ecosystems (the only two ecosystems with sufficient sample sizes). Adding intermediate predators to assemblages with top predators tended to result in greater prey suppression when the intermediate predator alone had larger effects on prey. However, this pattern was weak (but significant) for terrestrial invertebrates and nonevident for lentic ecosystems (Fig. 3C). Variation among studies in relative suppression with top predators alone was smaller than with intermediate predators, so the top predator's performance in suppressing the shared prey when tested alone was a relatively poor predictor of the observed influence of adding a top or intermediate predator to create a three-species IGP module (Fig. 3B, D).

There were no significant linear relationships between experiment duration and any of the resulting effect sizes, or between the area of the experiment venue and any of the resulting effect sizes. However, the slope of the regression between area and E_{TP} was marginally significant ($P = 0.055$), and positive.

DISCUSSION

Three main results emerge from our analyses: (1) increased intraguild predation decreases prey suppression, (2) intermediate predators are often more effective than top predators at suppressing prey when alone, and as a result (3) indirect effects of the top predator have strong releasing effects on prey, as predicted by trophic cascade theory. These results are best supported by data from terrestrial invertebrate ecosystems, whereas patterns from aquatic ecosystems are often highly variable. To interpret our results, we now consider two general questions. First, do the results from terrestrial invertebrate ecosystems differ from other ecosystems because of differences in statistical power, differences in the way experiments are conducted in these ecosystems, or differences in the role of IGP in these communities? And second, what can short-term studies tell us about equilibrium based IGP theory?

Statistical power may have influenced our ability to detect differences among ecosystems because ecosystems differed in the number of studies with documented unidirectional IGP. Multiple predator experiments with terrestrial invertebrates often included unidirectional IGP, while it was often unclear whether multiple predator experiments in lotic ecosystems included unidirectional IGP (thus these experiments were excluded from our analyses). Lentic ecosystems were much more evenly represented by experiments with and without IGP. Relatively few marine and terrestrial vertebrate experiments have been conducted examining questions about prey suppression or prey release with IGP. Thus, small sample sizes in many ecosystems limit our ability to draw strong conclusions about the biological or experimental sources of variation between ecosystems in our meta-analyses.

Beyond differences in sample size among ecosystems, there may also be differences in the way experiments were conducted in the various ecosystems. For example, the sizes of the experimental venues or duration of the experiments might differ. The sizes of the experimental venues used in the various ecosystems ranged from quite small in lotic ecosystems (mean = 0.81 m^2) to fairly large in marine ecosystems (mean = 10.4 m^2). However, this size difference does not seem to account for the variation in the magnitude of our effect sizes among ecosystems (see *Results*). The experiments were also conducted at different temporal scales in different ecosystems. For example, the mean experiment duration was longer for lentic ecosystems than it was for terrestrial invertebrate ecosystems, the two ecosystems for which we had the most data (41.7 days [range: 1.0–127] in lentic ecosystems and 27.2 days [range: 1.85–61] in terrestrial invertebrate ecosystems). We know that experiment duration itself was not significantly related to the effect sizes (see Results: but see Osenberg et al. 1999), but it is possible that the interplay between experiment duration and mean generation time differed among ecosystems in such a way to explain the effect size differences. Experiments in terrestrial invertebrate ecosystems often focused on organisms with generation times less than 30 days, whereas experiments from lentic ecosystems varied

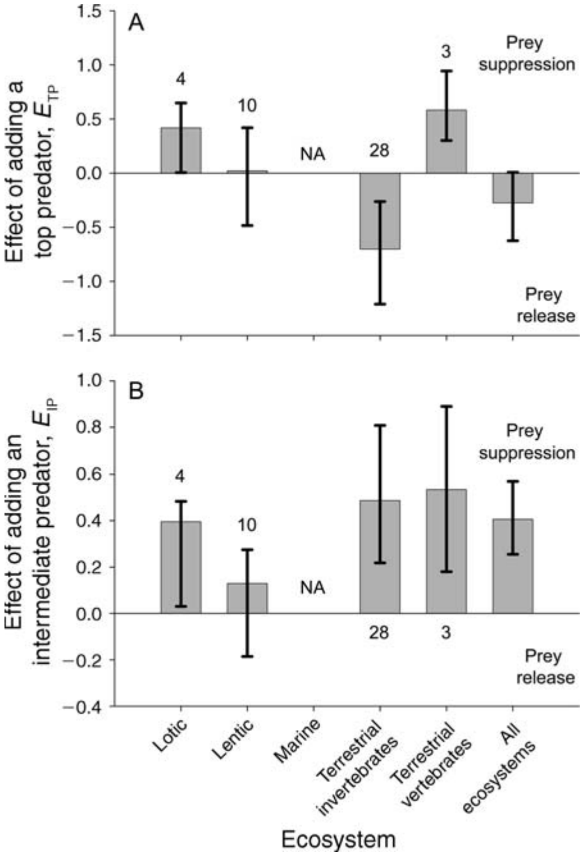

FIG. 2. (A) The effect on prey density caused by adding a top predator to an assemblage with the intermediate predator (E_{TP}, Eq. 4). (B) The effect on prey density caused by adding an intermediate predator to an assemblage with the top predator (E_{IP}, Eq. 5). All values are means ± bootstrapped 95% CI. Positive values indicate prey suppression, whereas negative values indicate prey release. The number above or below each bar gives the number of studies used to calculate the mean. NA designates cases in which the sample size was less than two.

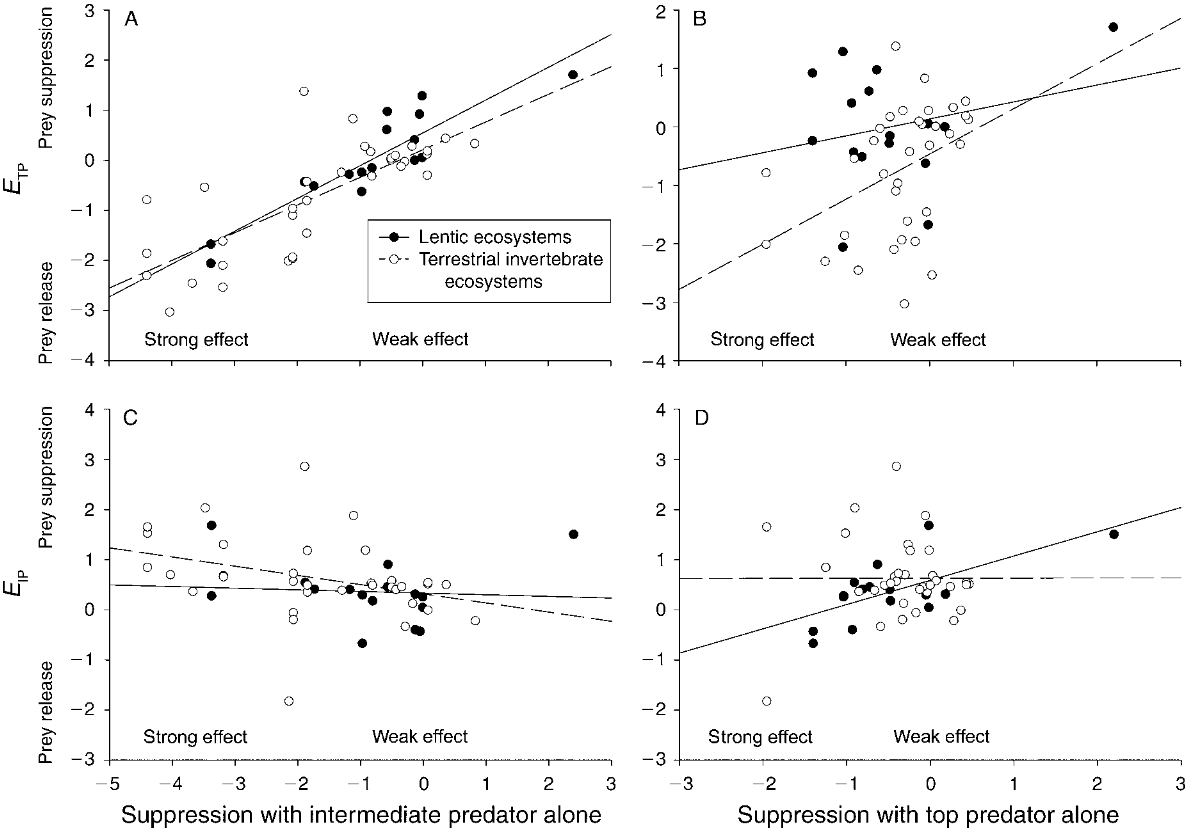

FIG. 3. (A) Relationship between E_{TP} (effect of adding a top predator, Eq. 4) and S_{IP} (relative suppression with intermediate predator alone, Eq. 6). For lentic ecosystems, slope = 0.654, Monte Carlo critical values are −0.0826 and 0.3185; for terrestrial invertebrate ecosystems, slope = 0.552, Monte Carlo critical values are −0.1316 and 0.0743. (B) Relationship between E_{TP} and S_{TP} (relative suppression with top predator alone, Eq. 7). For lentic ecosystems, slope = 0.290, Monte Carlo critical values are −0.6012 and 0.5714; for terrestrial invertebrate ecosystems, slope = 0.773, Monte Carlo critical values are −0.6778 and 0.6411. (C) Relationship between E_{IP} (effect of adding an intermediate predator, Eq. 5) and S_{IP}. For lentic ecosystems, slope = −0.033, Monte Carlo critical values are −0.2230 and 0.2304; for terrestrial invertebrate ecosystems, slope = 0.183, Monte Carlo critical values are −0.1669 and 0.1756. (D) Relationship between E_{IP} and S_{TP}. For lentic ecosystems, slope = 0.485, Monte Carlo critical values are −0.1115 and 0.1404; for terrestrial invertebrate ecosystems, slope = 0.002, Monte Carlo critical values are −0.0709 and 0.0778).

widely between studies focusing on zooplankton prey (with short generation times) vs. fish or amphibian prey (with much longer generation times). As a result, it was possible for more of the terrestrial invertebrate studies to experience multiple generations than experiments in lentic ecosystems. However, the number of generations encompassed by the terrestrial invertebrate studies was still relatively small.

The opposing results of adding a top predator to lotic or terrestrial vertebrate vs. terrestrial invertebrate ecosystems (Fig. 2A) may suggest that the architecture of the food webs and role of indirect effects differs between these ecosystems. For example, the increase in prey suppression with the addition of a top predator in lotic and terrestrial vertebrate ecosystems may be evidence of V-shaped food webs in which exploitative competition is important because of the amount of direct consumption of the shared prey by the top predator. Terrestrial invertebrate ecosystems, in contrast, may show an increase in prey release with the addition of a top predator because they have more linear food webs, with the top predators consuming the more effective intermediate predators.

If food web architecture differs between terrestrial invertebrate ecosystems and other ecosystems, then the likelihood of behavioral effects (such as the presence of trait-mediated effects) may also differ among ecosystems. In addition to density-mediated effects in linear food webs, the top predators may reduce the foraging activity of the intermediate predator, a trait-mediated effect (Preisser et al. 2005). This behavioral shift would further reduce the intermediate predator's ability to suppress the prey population in ecosystems with linear food webs, such as terrestrial invertebrate ecosystems. These trait-mediated effects would be much less likely to play a significant role in ecosystems with V-shaped food webs, such as lotic and terrestrial vertebrate ecosystems.

Although a recent cross-ecosystem comparison of trophic cascades found that predator effects were strongest in lentic ecosystems and weakest in terrestrial

PLATE 1. A crab spider (Thomisidae) eating an assassin bug (*Zelus renardii*) in a cotton field. Both species are predators of many invertebrates in cotton fields. Photo credit J. A. Rosenheim.

food webs (Shurin et al. 2002), our strongest (and least noisy) results were often found with terrestrial invertebrate ecosystems. Lentic ecosystems were quite variable in our effect size measures. The differences in these conclusions likely stem from the differences in our inclusion criteria. We focused on assemblages with multiple predator species and a shared animal prey, while Shurin et al. focused on the responses of herbivores and plants to predators. Our focus on unidirectional IGP also restricted the number of papers that we included.

What can short-term studies tell us about equilibrium based IGP theory? IGP theory is based on long-term equilibria, so ideally it would be tested using data from long-term experiments that allow the component species to reproduce and settle in their equilibrium densities. In reality, most experiments examining IGP focus on short-term survival or population growth rates of the prey and predators. These transient dynamics do not necessarily translate into predictable long-term equilibrium densities (see Briggs and Borer 2005). However, the analysis of these shorter-term experiments allows us to draw conclusions about systems that are dominated by transient, non-equilibrial dynamics. These systems are widespread in nature, since many systems do not reach equilibrium. Moreover, short-term experiments may be connected in some way to equilibrium models if the predator and prey densities used in experiments approximate the equilibrium densities in nature. Typical field densities may reflect information about the key parameters that describe prey and predator equilibria (e.g., the prey's population growth rate, the predator's attack and death rates, and the predator's efficiency at converting prey to offspring). If so, then experiments using these natural densities may come closer to revealing which predators could drive the prey to a lower, stable equilibrium by examining short-term responses.

Ecologists have long been interested in whether multiple predator assemblages suppress prey populations more than single predator assemblages (see review in Sih et al. 1998). This question has particular relevance to biological control (Hassell and Varley 1969, Murdoch et al. 1985, Rosenheim et al. 1995). Our results emphasize the importance of knowing whether or not IGP occurs in a given assemblage. If IGP does not occur, then it is likely that releasing multiple control agents will provide better suppression of the pest population than a single control agent. However, if either unidirectional or mutual IGP may occur, it is more likely that the single best control agent will be more effective at suppressing the prey population than multiple control agents combined.

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APPENDIX A

A list of all papers used in the meta-analytic calculations (*Ecological Archives* E088-164-A1).

APPENDIX B

Summary statistics based on IGP type and ecosystem (*Ecological Archives* E088-164-A2).

SUPPLEMENT

Data used for the statistical analyses (*Ecological Archives* E088-164-S1).