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Author(s): Jessica Gurevitch, Janet A. Morrison, and Larry V. Hedges

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The Interaction between Competition and Predation: A Meta-analysis of Field Experiments

Jessica Gurevitch,^{1,*} Janet A. Morrison,^{2,†} and Larry V. Hedges³

1. Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794-5245;

2. Department of Biology, College of New Jersey, P.O. Box 7718, Ewing, New Jersey 08628-0718;

3. University of Chicago, Chicago, Illinois 60637

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ABSTRACT: Ecologists working with a range of organisms and environments have carried out manipulative field experiments that enable us to ask questions about the interaction between competition and predation (including herbivory) and about the relative strength of competition and predation in the field. Evaluated together, such a collection of studies can offer insight into the importance and function of these factors in nature. Using a new factorial meta-analysis technique, we combined the results of 20 articles reporting on 39 published field experiments to ask whether the presence of predators affects the intensity of competitive effects and to compare the average effects of competition and predation. Across all studies, the effects of competition in the presence of predators were less than in the absence of predators, and the interaction between competition and predation for most response variables was statistically significant. Removal of competitors had much more positive effects on organisms' growth and mass than did exclusion of predators. Predator exclusion had much more beneficial effects on organisms' survival than did competition. The mean effects of competition and predation on density did not differ from one another. The results differed among trophic levels. Further understanding would benefit greatly from more field experiments that manipulate both competition and predation, that focus on a wider range of organisms and environments, that focus on population-level parameters such as density, and that report results more completely, including data such as sample sizes and variances.

Keywords: meta-analysis, ecological experiments, statistical interaction, predation, competition, herbivory.

* To whom correspondence should be addressed; e-mail: jgurvitch@life.bio.sunysb.edu.

† E-mail: morrisja@tcnj.edu.

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Field experiments can offer profound insights into the importance of factors structuring ecological communities. While the limitations of ecological field experiments are well known (e.g., Hurlbert 1984; Hairston 1989; Scheiner 1993; Huston 1997; Underwood 1997), in most cases they provide the only means by which we can test hypotheses regarding the existence and strength of forces that are proposed by theory or observation to have a substantial influence in nature. It is clear that a wide spectrum of interactions between species occurs in natural systems. Competition and predation are generally believed to be among the most important of these in most communities, and they also have the potential to interact with one another. There have been many experimental field studies on competition or predation (e.g., Connell 1983; Schoener 1983; Sih et al. 1985; Gurevitch et al. 1992), including some studies that investigated both competition and predation (Sih et al. 1985).

The purpose of this article is to survey field experiments in which both competition and predation have been manipulated in the same factorial experiment, so that we can judge the relative importance of competition and predation in natural systems and assess the magnitude and direction of their interaction. As our understanding of the forces shaping community structure has matured, two related important debates have emerged; they are centered on whether communities tend to be structured by equilibrium or nonequilibrium processes and on whether they are under “bottom-up” or “top-down” control. Our study of the relative strengths of competition, predation, and their interactions in natural communities can offer insight into both of these issues. We evaluate the results of our survey quantitatively with a new statistical technique—factorial meta-analysis. The application of this technique to evaluate studies of competition and predation is an example of the potential usefulness of factorial meta-analysis in many multifactor questions in ecology.

In recent years, many ecologists have favored nonequilibrium theories of community structure over older equilibrium theories that stressed the role of competition

in particular (Chesson and Case 1986). Many stochastic processes that influence community structure have now been identified. For example, variation over time and space in recruitment can have unpredictable but profound consequences in determining community structure (e.g., Booth and Brosnan 1995). Other stochastic influences that appear important for community structure include variation in productivity and physical stress (influenced by weather, etc.) and various forms of abiotic and biotic disturbance (Pickett and White 1985; Chesson and Case 1986; Menge and Sutherland 1987; Sugihara 1995; Grossman et al. 1998). One of the critical aspects of this shift toward a nonequilibrium view is the assumption that stochastic variation in disturbance, recruitment, etc., alters competitive interactions, which otherwise would still be a main determinant of community structure. Instead, it is thought that the unpredictable variation in such factors promotes a temporally and spatially shifting community structure. An important goal in community ecology, then, is to determine how nonequilibrium factors may interact with competition to influence its outcome.

Of all of the factors that encourage this nonequilibrium view of community structure, disturbance has received perhaps the greatest attention by researchers (Pickett and White 1985). Predation can be thought of as a disturbance factor under some circumstances. While predation can directly effect prey population sizes, the importance of predation in community structure may also be via its role as an agent of disturbance. Under this scenario of predator-mediated coexistence among competitors at a lower trophic level, predation on superior competitors prevents competitive exclusion, allowing inferior competitors to become established, to survive, and to reproduce (Paine 1966; Caswell 1978). Recent examples lend support to this idea. For example, Wootton (1992) suggested that, among other direct and indirect effects in an intertidal community, predation by gulls on sessile invertebrates reduced the effects of competition for space on algal species. Hambäck (1998) developed a model that demonstrated that an herbivore foraging optimally can promote the coexistence of plant competitors in a seasonal environment and presented data to show that foraging by voles can alter the competitive dominance of bilberry over lingonberry. Many other similar observations have been made in the literature, and enough studies have now been done to allow for a synthetic analysis of how predation alters the outcome of competition. With the technique of factorial meta-analysis presented below, we can quantitatively assess, for the first time, the strength of the interaction between competition and predation across many different studies.

Another reason for focusing our meta-analysis specifically on the interaction between competition and predation is the pragmatic one of the availability of data. Ideally,

studies should integrate all of the factors that may be responsible for organizing communities, so that we can determine their relative strengths and examine how they interact. At this time, however, the data for such a project do not exist because it would require experimental multifactorial studies that manipulate these factors together in the same communities, and many such studies from many different systems are needed in order to make generalizations. Field experiments that include even two factors together are uncommon enough, and studies that include more than that are rare indeed. Because there are a large number of field experiments on competition and because a fair number of these also include predation, this article offers a first step in that direction by examining those studies that manipulate competition and predation together.

We view the technique of factorial meta-analysis as particularly useful for addressing questions about the interaction between factors (here, competition and predation), but because the studies necessarily include manipulations of both factors in the same experiment, the technique can also be used to compare the overall strength of the effect of competition with that of predation. This latter issue continues to be debated in ecology. Through the 1970s, theories of community organization that considered competition to be the main organizing force in communities were favored, leading to predictable species assemblages and relative abundances, and classic experiments were done that seemed to confirm the strong effects of competition (Connell 1983; Schoener 1983; Gurevitch et al. 1992). While the focus of much of current research has shifted, scrutiny of competition as an organizing force in communities can provide useful insight into the current question of bottom-up versus top-down control of communities and food webs (Hunter and Price 1992; Power 1992; Hassell et al. 1998).

The work indicating the strong effects of competition in natural communities also implies that trophic webs are controlled from the bottom up; competition for resources is the important factor determining community structure at the lower levels, and these effects are transmitted to the higher trophic level communities that feed on them (Hunter and Price 1992; Rosemond 1993; Chen and Wise 1999). Increasingly, however, a greater role has been argued for predation and herbivory in structuring communities. These ideas, like those that emphasize the importance of competitive interactions, are based on both well-established equilibrium theory as well as empirical work (Rosenzweig and MacArthur 1963; McNaughton 1985; Crawley 1989; Strong 1992; Wootton et al. 1996; Sih et al. 1998). From this, a top-down view of trophic webs has emerged (Strong 1992; Floyd 1996; Dyer and LeTourneau 1999), suggesting that by directly controlling population

sizes of prey, predation is the critically important factor structuring communities. Our meta-analysis of studies that manipulate both competition and predation in field experiments provides a method to reach quantitative generalizations about the relative importance of the two factors for the first time.

The debate about competition and predation has attracted greater or lesser amounts of attention in different ecological subdisciplines. It is especially well developed for aquatic systems, for example, where both types of interactions can be very strong (e.g., Sih et al. 1985; Persson 1999). There is not likely to be one universal answer to this debate for all of nature. Meta-analysis allows us not only to test the relative importance of competition and predation across all study systems but also, if the data are sufficient, to analyze and to compare these effects for particular groups of organisms.

To date, the ability to reach general conclusions from the results of field experiments about the relative importance and magnitude of competition and predation and the degree to which they interact with one another has been limited. The limitations are caused mostly by lack of the right kinds of data, but also by the lack of, until recently, tools for data synthesis that are both powerful and appropriate. Sih et al. (1985) reviewed field experiments on predation and compared their outcomes with those on competition. They concluded that both factors were generally important but that their effects were relatively equivalent, except in the case of terrestrial plants, in which herbivory was more important than competition. They emphasized that many more experimental studies were needed in which both factors would be manipulated with well-replicated factorial designs.

Sih et al. (1985) used "vote counts" (counts of the number of statistically significant results) to assess the results of their survey, no doubt because that appeared to be the best method to use at that time, but it is now understood that this approach is statistically flawed and can result in serious inaccuracies (see, e.g., Hedges and Olkin 1985; Gurevitch and Hedges 1993). Other surveys on the importance of competition in field experiments have also used vote counting (Connell 1983; Schoener 1983; Goldberg and Barton 1992). In contrast, Gurevitch et al. (1992) used meta-analysis, a more powerful and more accurate statistical approach, to analyze the results of field experiments on competition but did not address predation or its interaction with competition.

Meta-analysis avoids the problems associated with vote counting and is a much more powerful and accurate approach to quantitative data synthesis. In brief, modern meta-analysis methods depend on calculating a standardized measure of the magnitude of an effect of interest from a number of independent studies and determining a con-

fidence interval around that effect size. One might wish, for example, to examine the responses of different organisms to the removal of competitors, and the standardized effect size in each study would be a measure of the magnitude of that response. These standardized effect size measures are then weighted by the inverse of their sampling variances, which depend on sample size, and then the weighted mean effect size across studies is calculated. Studies may then be partitioned into meaningful categories to account for explanatory variables (e.g., to assess the differences in the effect among trophic levels, etc.) by various methods and the agreement—or lack thereof—among studies is assessed. Meta-analysis is gaining increasing attention in ecological and evolutionary research syntheses (e.g., Arnqvist and Wooster 1995; Osenberg et al. 1999). Recent meta-analyses in ecology and evolution have examined a wide diversity of questions including, for example, adaptive deme formation in phytophagous insects (Van Zandt and Mopper 1998), the effects of elevated CO₂ on woody plants (Curtis and Wang 1998), and the effects of marine nutrient-enrichment experiments on phytoplankton (Downing et al. 1999).

We propose a meta-analysis approach to analyze a series of two-factor experiments (each with two levels) to quantify the average effects of each of the two manipulated factors, competition and predation, as well as their interaction. Previously, although there have been thousands of meta-analyses published in medicine and in the social sciences, and close to several dozen in ecology and evolutionary biology (J. Gurevitch, unpublished data), meta-analysis has only been used to summarize the results of single-factor experiments (Cooper and Hedges 1994; but see Hechtel and Juliano 1997). Our approach to carrying out a factorial meta-analysis is analogous to factorial ANOVA within single experiments. As in factorial ANOVA, one can examine the magnitude and statistical significance of the main factors (here, competitor removal and predator exclusion) and of their interaction (i.e., the effect of predator exclusion on the response to competitors). We outline our approach to factorial meta-analysis below (see "Methods") and provide details of the calculations in the appendix.

Unfortunately, many of the studies published on the interaction between competition and predation do not meet the minimum requirements that are needed to quantify the relative magnitude of competition, predation, and their interaction. Most importantly, it is necessary to have manipulated both competitors and predators in the same experiment in a well-replicated factorial design (Sih et al. 1985). Many studies found by Sih et al. and more recent articles that we found failed to meet these criteria and could not be used. These included studies in which competition was manipulated in one experiment, and preda-

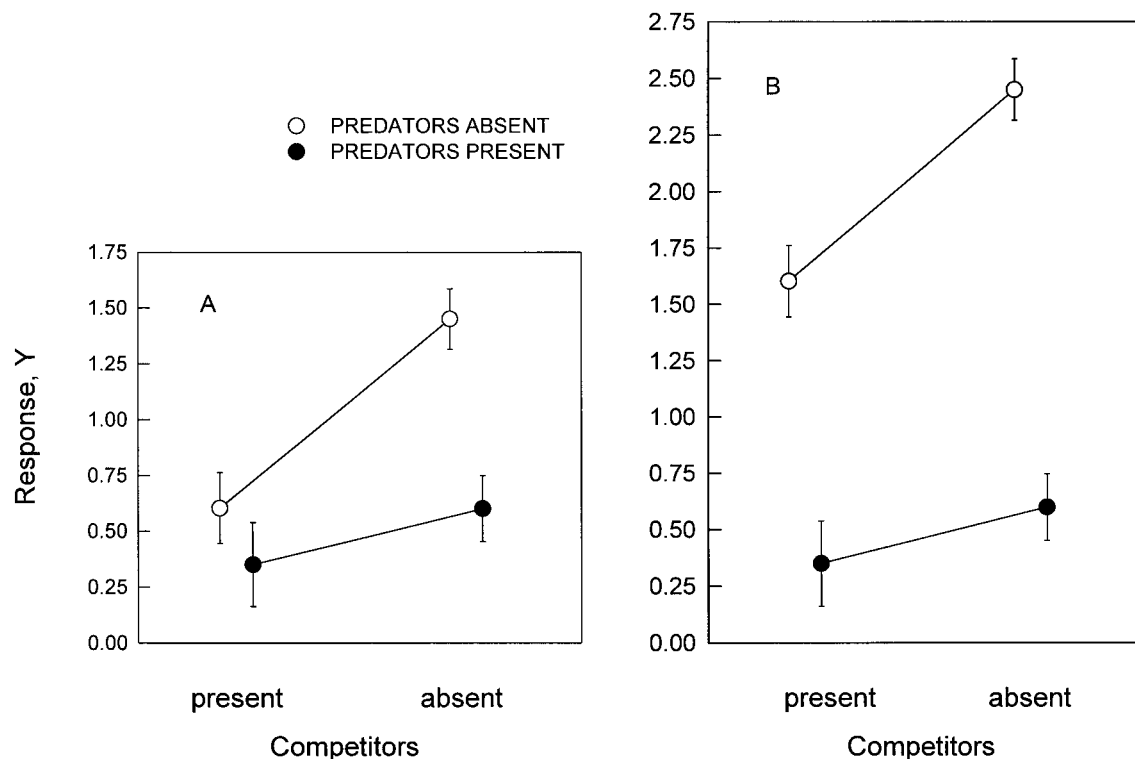


Figure 1: Interaction diagrams for fictitious data on organisms experiencing two levels of competition (competitors present and absent) and two levels of predation (predators absent and present) in a factorial experiment. The measure of response, *Y*, is on an arbitrary scale of performance in which higher numbers indicate that the organisms are benefiting. The effects of the absence of competitors are the same in both A and B, but the effects of the absence of predators are larger in B than in A (see text).

tion in another separate experiment, as well as others in which one of the factors was manipulated and the other was merely observed (but not manipulated experimentally). While it would be very valuable to have a greater number of appropriate studies available, our search of the literature provided sufficient data to do a meaningful meta-analysis that allowed us to test in a general way some of the major theoretical predictions regarding competition, predation, and their interaction. All of our results are measures of the strength and direction of the effects of competition and predation in experimental field studies. Most of the studies were simple short-term studies at relatively small spatial scales on single target species (although sometimes the same article reported on the results of more than one experiment, each with a different target organism, different predator, or different competitor). One might or might not then wish to extrapolate from these field experiments to draw conclusions about the roles of competition and predation in determining community structure in nature.

It is important to note that our interpretation of the results of tests of statistical interactions differs somewhat

from the conventional approach (e.g., Sokal and Rohlf 1981, p. 329; Zar 1996, p. 246). Ecologists are often taught in introductory statistics classes that if an interaction term is significant, the main factors are impossible to interpret and are essentially meaningless. While this may sometimes be true, it is not necessarily true. For example, if both factors have a positive effect on the outcome, but one level of one of the factors results in a much stronger response to the second factor, the statistical interaction will be significant; but one can also legitimately say that the two main factors also have positive effects on the response. We illustrate this with a hypothetical example using a classical interaction diagram (fig. 1A, 1B). Imagine an experiment with a standard factorial design in which there were two factors, each at two levels. The first factor might be the presence or absence of competitors and the second factor, the presence or absence of predators. With simulated data for illustrative purposes, one can see that, in this hypothetical experiment, the upper line in figure 1A (predators absent, *open circles*) goes up more steeply than the lower line (predators present, *closed circles*). That is, when predators were excluded, there was a much stronger response

to the removal of competitors than when predators were present. The response to these two factors, competition and predation, is a statistical interaction, one of various possible kinds of interactions between factors. However, it still seems reasonable to say that there was a positive response to both the absence of predators and to the absence of competitors, even though these two factors interact. It may also be informative to compare the magnitude of the main effects of the two factors, even though they interact. In figure 1A, competitor removal and predator exclusion had approximately equally large effects on the outcome. However, in figure 1B, it is clear that predators had a much larger quantitative effect than did competitors. It is only when the lines in an interaction diagram cross that a statistical interaction makes it difficult to say anything about the main effects.

With a factorial meta-analysis we can test the following predictions about the relative importance of competition, predation, and their interaction. Prediction 1: nonequilibrium models of community structure suggest that disturbance caused by predators will disrupt competitive interactions and lead to coexistence of species. Under this exploiter-mediated coexistence model, experimental studies should show a strong statistical interaction between competition and predation, with the effect size and/or direction of competition different with and without predators present. Prediction 2: models of resource-based competitive exclusion suggest that competition is the main structuring force in a community, resulting in bottom-up control of community structure. In that case, experimental studies should show a large effect for competition. If competition is more important than predation, the effect size of predation should be small relative to competition. Of course the studies we have included in our meta-analysis can only address current demonstrable competition and say nothing of the possible strength of past competition and its role in structuring the communities under study (Connell 1980). Prediction 3: top-down models suggest that predation is more important than competition. In that case, experimental studies should show a large effect for predation. If predation is more important than competition, the effect size of competition should be small relative to predation.

Methods

Studies which met the criteria above for factorial experiments were included in the meta-analyses. In addition, we used only field experiments. This excluded experiments done in greenhouses and laboratories but did include studies done in containers placed in the field. Because predator densities were manipulated in these experiments, most of them involved some sort of cages, tubs, or pens placed in

the field. In most cases, competition was interspecific but, in some cases, intraspecific competition was studied. Finally, published results must have included treatment means, sample sizes, and standard deviations or other measures of variation from which standard deviations could be calculated (see Gurevitch et al. 1992). If the published article did not include these data but met the other criteria, we attempted to contact authors where possible to obtain the missing data. Studies were excluded if we could not obtain these summary statistics, even though the experiments appeared to be appropriate. In a few cases, additional unpublished data or data published in journals not covered by our literature search were provided by the authors we contacted, and we included those data if they otherwise met our inclusion criteria.

We began our literature search by including those articles covered in the review by Sih et al. (1985) in which competition and predation were both manipulated experimentally, assuming that this review had identified most of the usable studies published prior to 1985. We then surveyed eight journals for approximately 10 yr, from January 1985 (when the coverage included by the aforementioned review ceased) until June 1995. The journals we examined were *The American Naturalist*, *Copeia*, *Ecological Monographs*, *Ecology*, *The Journal of Animal Ecology*, *The Journal of Ecology*, *The Journal of Experimental Marine Biology and Ecology*, and *Oecologia* (Berlin). In addition, we reviewed a comprehensive literature survey that had been done previously for a meta-analysis of field competition experiments (the results of which were published in part by Gurevitch et al. 1992). For each article in that data set, it had been noted if predation had been manipulated; where appropriate we included those articles in our survey.

Data Management

Data from each article were entered into spreadsheet files with all related information that might be relevant to the comparisons (system, latitude, trophic level of competitors, etc.). We created four separate data sets to correspond to four common categories of response variable: growth and mass (measured as properties of individuals) and survival and density (measured as properties of populations). A separate meta-analysis was done for each of these four response variables. Some articles reported on the results for more than one responding species or for more than one experiment. In this case, each responding species was included in the meta-analysis; separate experiments reported in a single article might also all be included. If an article reported results from a single experiment for more than one response variable (e.g., growth, survival), those results would not be included in the same meta-analysis but could potentially be included in more than one of the

Table 1: Design of the 2×2 factorial meta-analysis used in this study

	Predators present	Predators absent
Control	Competitors at natural density	Competitors at natural density
Experimental	Competitors at manipulated density	Competitors at manipulated density

four meta-analyses we performed. If an article reported results over the course of the experiment, we used only the results at the end of the experiment. A single experiment was thus represented only once in any single meta-analysis for a given responding species.

We organized the data into four treatment combinations representing a 2×2 factorial design (table 1). Some studies contained enough information to calculate only three of the four cells in table 1 but were judged, nonetheless, to provide valuable data and so were included. Most of the competitor manipulations were complete removals. In the few cases where the manipulation involved the enhancement of competitor densities, the sign in the calculation of effect sizes was reversed (see Gurevitch et al. 1992 and appendix). That is, in all cases a positive effect size indicates that lower competitor density had a positive effect on the target organism, as predicted. Predator manipulations were generally complete removals or exclusions, although in a few cases predators were initially absent and were supplemented as an experimental treatment. The analyses compared treatments in which predators were absent with those where predators were present, regardless of whether the experimental treatment was to exclude predators or to add them where they were initially absent. Positive effect sizes in response to predator exclusion indicate that removal of predators had a positive effect on the prey, as predicted. We used the common meta-analysis metric of standardized effect size, Hedges's d . Essentially, d is a measure of the difference between the experimental and control means divided by a pooled standard deviation and multiplied by a correction factor to account for small sample size bias. There are some good arguments for using other metrics (e.g., Osenberg et al. 1997), but we chose to use this conventional metric because the standardized difference in performance made sense to us ecologically and in the context of experimental design and because it is closely related to the common statistical tests (t -tests and ANOVAs) used to analyze the experiments we were synthesizing.

Calculations and Analysis

For each study we calculated the effect size of competitor removal and its sampling variance when predators were present (d_p and $\hat{s}^2[d_p]$) and when they were absent (d_a and $\hat{s}^2[d_a]$). The effect sizes and variances were calculated on a spreadsheet according to a standard approach (e.g.,

Hedges and Olken 1985; Gurevitch et al. 1992), with modifications caused by the factorial design of the experiments as detailed in the appendix. We also modified the conventional approach (e.g., see Gurevitch and Hedges 1993) to calculating weighted mean effect sizes because of the factorial nature of the experiments (see details in the appendix). In addition, the interpretation of the average effects of competitor removal, predator exclusion, and of their interaction across studies may be somewhat unfamiliar. The overall effect of predator (or herbivore) exclusion is the difference between the sum of the means of the two treatments where predators were excluded (table 1) and the sum of the two treatments where predators were present (i.e., when the competitor treatments are ignored; see formula for d_H in the appendix). In table 1, this would be equivalent to adding the means for the two treatments on the left (predators present, competitors at natural and manipulated density) and subtracting them from the sum of the two means on the right (predators absent, competitors at natural and manipulated density). The overall effect of competitor removal is the difference between the sum of the means of the two treatments where competitors were present (table 1) and the sum of the two treatments where competitors were removed (that is, when the predator treatments are ignored; see formula for d_R in the appendix). In table 1, this is equivalent to subtracting the sum of the means for the treatments in the top row (competitors at natural density, with predators present or absent) from those in the bottom row (competitors at manipulated density, predators present or absent). This is similar conceptually to what one does in assessing main effects in a factorial ANOVA. The magnitude of the interaction is calculated and assessed as an effect size itself (i.e., the mean interaction across studies, d_{t+} , may be small, intermediate, or large, as is any mean effect, d_+), and the interaction is judged to be significantly >0 if the confidence interval (CI) around that effect does not overlap 0 (see appendix). A positive value for the interaction term indicates that competition has a greater effect in the absence of predators than in their presence (the expected direction). We omitted the results of a single study (Lively and Raimondi 1987) from the calculation of the average effects of predation. In this study, it appeared that the predator was exclusively preying on the competitor and not on the target species, and, in fact, there was a large negative response of the target organism to the exclusion of the predator. We felt, therefore, that it did not make sense to in-

clude this study in estimating mean predation effects on target organisms.

We used fixed-effects analyses for all statistical tests. The homogeneity of the group of studies contributing to the mean effect, d_+ , can be evaluated with a homogeneity statistic, Q . This statistic provides a test of the overall agreement, or lack of it, in the outcomes of the various studies. The homogeneity statistic Q has a χ^2 distribution in a parametric fixed-effects model (used here; see Hedges and Olkin 1985; Gurevitch and Hedges 1999). The total heterogeneity among studies, Q_T , can be partitioned into the heterogeneity among groups of studies, Q_B , and the heterogeneity among studies within each group, Q_W . The between-group heterogeneity provides a test of whether or not differences in the average effect size between groups of studies differs (e.g., do plants differ from anurans in their responses?).

We illustrate the results of the hypothetical example introduced in figure 1 in this context to demonstrate the interpretation of the results (fig. 2). Figure 2A (based on the data from the hypothetical experiment illustrated in fig. 1A) shows the effect sizes, d , of competition in the presence (*closed circle*) and the absence (*open circle*) of predators. The greater steepness of the top line (predators absent, *open circles*) in figure 1 is reflected in the larger

magnitude of the effect size in the absence of predators (fig. 2A, *open circle*; fig. 2A is identical whether based on the data in fig. 1A or on that in 1B). Figure 2B illustrates the overall effect of competitor removal across predation treatments (*square symbol*) and the overall effects of predator exclusion across competition treatments (*triangle*) calculated from the hypothetical data in figure 1A. These effects are approximately equal in magnitude. The overall effects of competitor removal across predation treatments (*square symbol*) and the overall effects of predator exclusion across competition treatments (*triangle*) in figure 1B are illustrated in figure 2C. Predator exclusion has a much smaller effect in figure 2B than in figure 2C, reflecting the differences between figure 1A and 1B. Predator exclusion in figure 1B also clearly has a much larger effect than competitor removal, and this is reflected in the larger effect size in figure 2C for predator exclusion in comparison with competitor removal. The overall effect of competitor reduction is the same for figure 1A and 1B, as reflected in the identical values for the overall effects of competitors in figure 2B and 2C. The interaction effect, calculated as shown in the appendix, is positive (competitors have a greater effect in the absence of predators) and about the same magnitude as the effect of competitor removal; the magnitude of the interaction effect is identical for figure

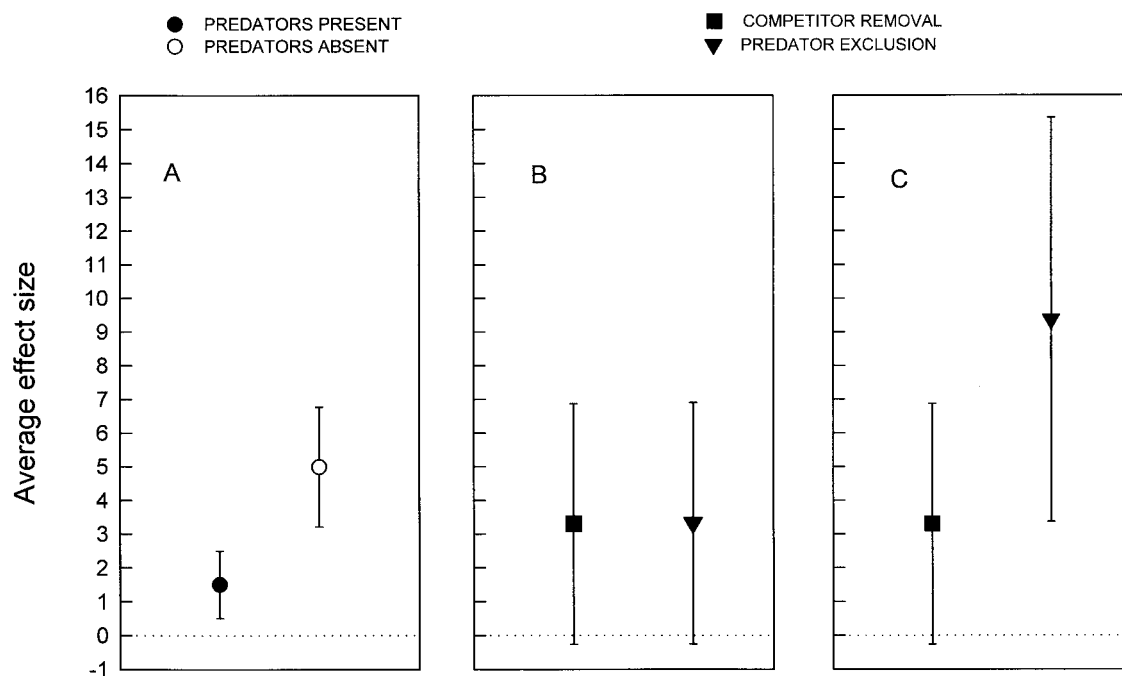


Figure 2: Based on the data for the fictitious experiment in figure 1. A, Average effect size of competition, d , in the presence of predators (*closed circle*) and in the absence of predators (*open circle*) with 95% confidence interval. B, Average effect size, d , of competition (*square symbol*) across predation treatments and average effect size of predation (*triangle*) across competition treatments from fictitious data in figure 1A (95% confidence intervals). C, As in B but with fictitious data from figure 1B.

Table 2: Articles used in the meta-analyses, with the measures of outcome and number of experiments indicated

Article	Measure of outcome	Number of experiments
Alford 1989	Mass	4
	Growth	4
Bergelson 1990	Mortality	2
	Mass	2
	Growth	2
Blois-Heulin et al. 1990	Mortality	2
Cortwright and Nelson 1990	Mortality	2
	Mass	2
	Growth	2
Dodson 1974	Density	1
Dungan 1986	Density	2
Harris 1987	Mortality	1
	Growth	1
Karban 1989	Mortality	1
Karban et al. 1994	Density	1
Lively and Raimondi 1987	Density	1
Lubchenco and Menge 1978	Density	2
Morin 1984	Density	3
	Growth	2
Morin 1986	Mortality	1
	Growth	1
	Mass	1
Morin 1987	Mortality	1
Parker and Salzman 1985	Growth	3
Peterson 1982	Growth	2
Reader 1992	Mortality	3
Smith and Cooper 1982	Density	2
Sredl and Collins 1992	Mortality	2
	Mass	2
	Growth	2
Wilbur and Faeth 1990	Mortality	4
	Mass	4
	Growth	2

1A and 1B. Keep in mind that figures 1 and 2 illustrate the results of a single experiment and that we have not yet addressed responses averaged across many experiments. Therefore, for a variety of reasons, including heterogeneity of effects across studies, the statistical significance of the mean interaction term across studies is determined as described in the appendix and may or may not be apparent by simply comparing effect sizes as in figure 2.

Results

We found 20 published articles that we were able to use. These articles included the results of 39 experiments (table 2). The experiments formed a somewhat eclectic collection of organisms and ecological situations. There were rela-

tively large numbers of published experiments on the interaction between competition and predation on anurans, often carried out in large outdoor cattle tanks but also in enclosures in natural ponds and lakes. There were moderate numbers of experiments on herbivory and competition on plants and scattered studies on other organisms. Almost all of the studies were carried out in temperate ecosystems, and none were conducted in the tropics. Studies were generally of rather short duration (growth, 2 mo–2 yr; mass, 2–8 mo; survival, 1 wk–7 mo; density, 8 d–6 mo).

Averaged across all studies, removing competitors had a greater effect in the absence of predators than when predators were present (fig. 3). The effects of competition in these field experiments were in all cases small to moderate and were always significantly >0 (i.e., CIs did not overlap 0), with the exception of effects on density. Competition had a small effect on density which did not differ from 0 in the presence of predators and a very large and significant effect on density in the absence of predators. The results are somewhat misleading for survival because they combine one group (anurans) that follows this pattern and another (plants) that does not (see below). The interaction term between competition and predation was significantly >0 for growth ($d_{1+} = 0.21$, CI = 0.13–0.29, $k = 17$; where k is the number of experiments) and density ($d_{1+} = 1.23$, CI = 0.63–1.82, $k = 9$) but not for mass of individuals ($d_{1+} = 0.01$, CI = -0.05 – 0.07 , $k = 12$). The in-

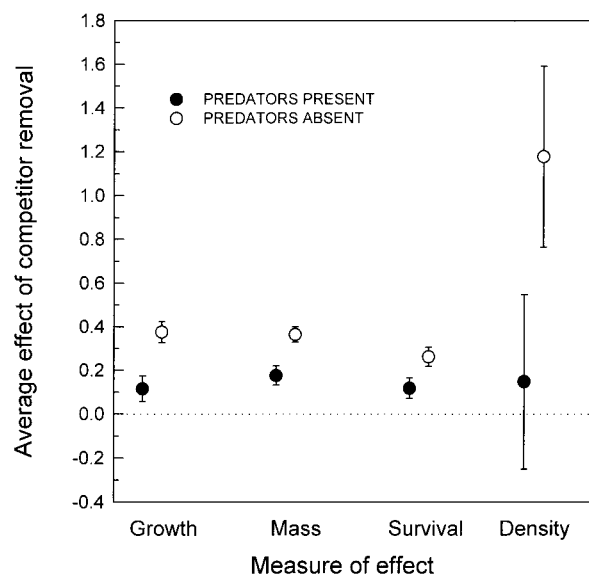


Figure 3: Average effect size of competition, d_{a+} or d_{p+} , across all studies (with 95% confidence intervals) in the presence (closed circles) and absence (open circles) of predators for meta-analyses on organisms' growth, mass, survival, and density.

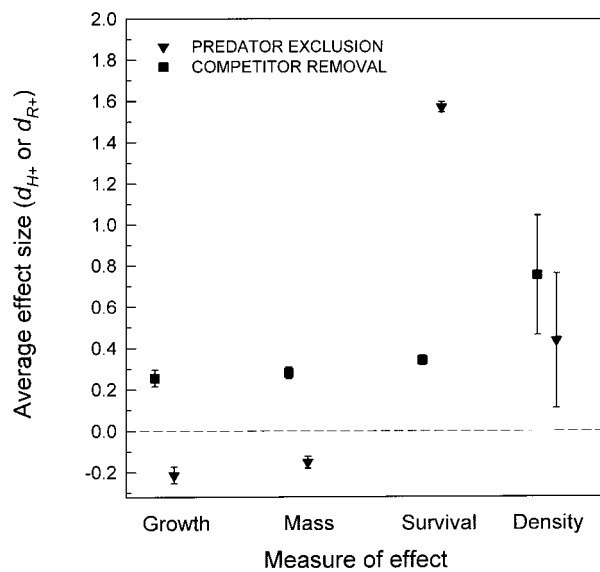


Figure 4: Overall average effect sizes of competition, d_{R+} (square symbols), and predation, d_{H+} (triangle symbols), for meta-analyses on organisms' growth, mass, survival, and density (95% confidence intervals).

teraction term had the opposite sign for survival ($d_{1+} = -0.06$, $CI = -0.16-0.03$, $k = 17$), although it was not significantly different from 0. The negative value indicates that removal of competitors had a smaller effect in the presence of predators than in their absence, in apparent contradiction to figure 3. This is because the mean effects for survival in figure 3 combine the responses of two groups (anurans and plants) that responded in very different fashion to the experimental treatments: the interaction term for anuran survival was positive ($d_{1+} = 0.69$, $CI = 0.39-0.99$, $k = 8$), in agreement with the other results, but was negative for plants ($d_{1+} = -2.57$, $CI = -3.13$ to -2.02 , $k = 5$; see fig. 7, below, and text discussing those results). The interaction term for survival differed significantly between anurans and plants ($Q_B = 24.5$, 1 df, $P < .001$).

The relationship between the average overall effects of removal of competitors and of predator exclusion differed, depending on the outcome that was measured. Removing competitors had moderately positive effects on growth and mass of individuals when the responses of all organisms were combined (fig. 4), while predator exclusion had moderately negative effects (i.e., organisms were smaller on average when predators were excluded). The effects of competitor removal and predator exclusion differed significantly (as indicated by the nonoverlapping confidence intervals) for both growth and mass. Excluding predators had a much larger effect on survival than did reducing competitors, on average, although both increased the sur-

vival of the target organisms. The effects of competitor removal and predator exclusion on density did not differ significantly (the 95% confidence intervals overlapped).

Almost all of the effects shown in figures 3 and 4 were heterogeneous, as indicated by significant values for the Q (homogeneity) statistic (tables 3, 4). There are at least two ways to view this heterogeneity. First, the studies may show heterogeneous outcomes, and efforts should be made to partition them into more meaningful categories (e.g., Hedges and Olkin 1985; Gurevitch et al. 1992). Second, these results may suggest that a fixed effects model, which assumes that all studies share a common effect size, is inadequate and, therefore, that a mixed model might better reflect the nature of the data (Gurevitch and Hedges 1999). We suspect that both of these points are valid in this case. However, a mixed model has not been developed for factorial meta-analyses, and so we retained the fixed-effects analysis while keeping in mind that heterogeneity of effects may not necessarily be very informative (as the additional variance component in a mixed-effects model is not taken into account in a fixed-effects model).

We therefore examined the data to see if there were ecologically reasonable ways of partitioning the data into potentially more meaningful classes of organisms or systems. While in many cases the studies were on a diffuse array of subjects that precluded some of the more potentially interesting and meaningful ways of subdividing effects across studies, in a number of cases there were clear ways to partition the studies. To examine responses further, studies on organisms' growth, mass, and survival were broken down into trophic categories. Because of the small number of studies in which density was measured, it was not possible to meaningfully partition those experiments.

We examine the results for growth, mass, and survival in turn. For those studies where growth was the measure of outcome, we separated the results into those on carnivores ($k = 4$ experiments), those on plants ($k = 5$) and those on anurans ($k = 9$; fig. 5). The interaction between

Table 3: Results of homogeneity tests for effects of competition for data shown in figure 3

Value tested	Predator	K	Q_T
Growth	Present	20	44.1*
Growth	Absent	19	1,479.3*
Mass	Present	13	583.6*
Mass	Absent	14	1,345.2*
Survival	Present	18	45.4*
Survival	Absent	18	10.5**
Density	Present	9	22.8*
Density	Absent	12	19.6**

* $P < .01$.

** P is not significant.

Table 4: Results of homogeneity tests for data shown in figure 4

Value tested	Effect	K	Q_T^*
Growth	Competition	17	734.0
Growth	Predation	17	986.9
Mass	Competition	12	1,015.2
Mass	Predation	12	1,278.7
Survival	Competition	17	119.8
Survival	Predation	17	383.8
Density	Competition	9	38.5
Density	Predation	8	95.0

* $P < .01$.

competition and predation did not differ significantly among these groups ($Q_B = 2.05$, 2 df, NS). The overall average effects of predator exclusion on growth differed among those groups, however (fig. 6; $Q_B = 46.11$, 2 df, $P < .01$), chiefly because elimination of predation/herbivory increased, on average, growth in carnivores and plants but had the opposite effect on anurans, decreasing their growth. The other measures for growth responses (average competition and competition in the presence or absence of predation) did not differ significantly among classes of organisms.

Experiments where organisms' individual mass was the measure of outcome were reported in substantial numbers only for anurans. We divided these studies on the effects of competition and predation on anuran mass into those in which there was interspecific competition ($k = 8$) and those in which there was intraspecific competition ($k = 3$; fig. 7). Interspecific and intraspecific competitive effects on anuran mass (i.e., mass of individuals) did not differ in the presence of predators ($Q_B = 1.04$, 1 df, NS) but differed substantially in the absence of predation, with intraspecific competition having much greater effects ($Q_B = 17.35$, 1 df, $P < .01$). The absence of predators had a much greater effect on intraspecific competition than on interspecific competition on anuran mass, resulting in a difference in the interaction between competition and predation between these two groups (fig. 7; $Q_B = 8.20$, 1 df, $P < .01$). The average effect of intraspecific competition was greater than that of interspecific competition as well ($Q_B = 9.14$, 1 df, $P < .01$), but the average effects of predator removal on individual mass were detrimental for anurans ($d_+ = -0.15$, CI = 0.18 to -0.12) and did not differ between intra- and interspecific groups.

Survival was measured in sufficient numbers of experiments only for plants ($k = 5$) and anurans ($k = 9$; fig. 8) to examine the results in more detail. Competitor removal in the presence of predators had large positive effects on plant survival and modest negative effects on the survival of anurans; the difference between plants and anurans was

significant ($Q_B = 15.05$, 1 df, $P < .01$). In the absence of predation, the effects of competitors on survival did not differ between the two groups ($Q_B = 1.47$, 1 df, NS). The interaction between competition and predation differed between the two groups. For plants, competitor removal had a large positive effect on plant survival only in the presence of predators. For anurans, competitor removal had beneficial effects only when predators were excluded ($Q_B = 98.00$, 1 df, $P < .01$). The average overall effects of the removal of competitors on survival (fig. 9) were positive and very large for plants but <0 (i.e., "competitors" aided survival) for anurans and differed between the two groups ($Q_B = 36.10$, 1 df, $P < .01$). The average overall effects of predator exclusion were very large for both plants and anurans and did not differ between these groups ($Q_B = 0.45$, 1 df, NS). On average, predation affected the survival of both plants and anurans much more than did competition.

Discussion

The patterns that emerge from this factorial meta-analysis are strikingly clear, make sense, and are relevant to larger issues of community structure. We first examine the results of the analysis of the interaction of competition and pre-

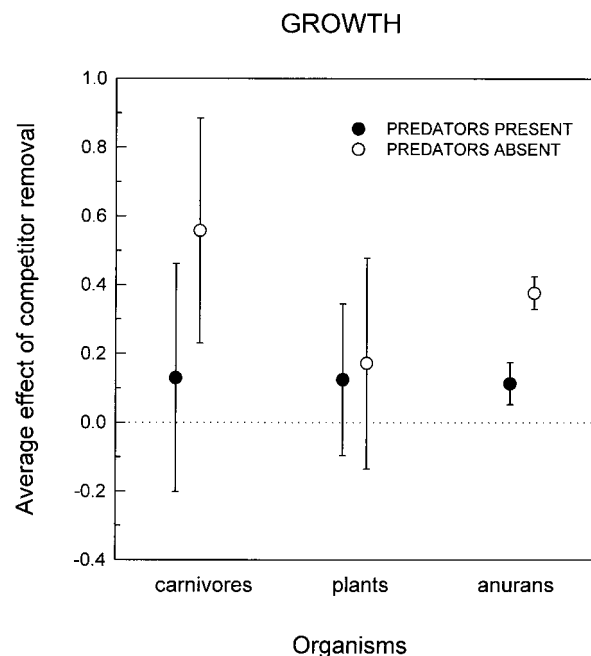


Figure 5: Average effect sizes, d_{+} or d_{p+} , of competitor removal on organisms' growth (95% confidence intervals) in the presence (closed circles) and absence (open circles) of predators. Results are shown separately for carnivores, plants, and anurans.

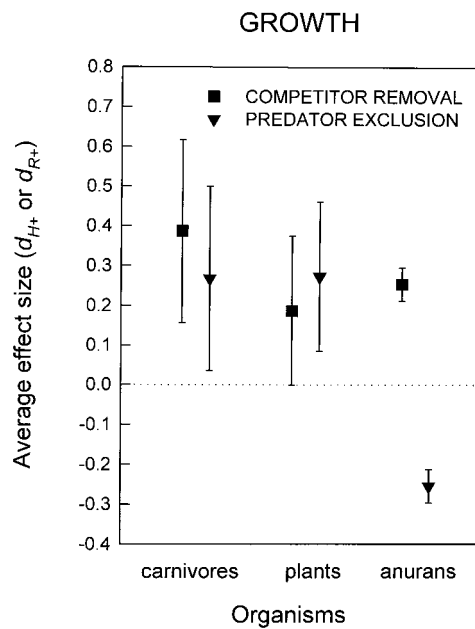


Figure 6: Overall average effect sizes of competitor removal, d_{R+} (square symbols), and predator exclusion, d_{H+} (triangles), on growth for carnivores, plants, and anurans (95% confidence intervals).

dation (prediction 1) and follow with a comparison of the overall effects of competition and predation as main factors (predictions 2 and 3). We will also evaluate several issues regarding the application of the technique of factorial meta-analysis to ecological research synthesis.

The analysis of the interaction of competition and predation in these field experiments showed that, in general, competitor removal had positive effects on the focal organisms both with and without predation but that it was more intense when predators were excluded, presumably because predation reduced the ability of the strongest competitors to dominate. This finding supports our first prediction and the idea that, in general, predation may act to reduce the intensity of competitive interactions. By weakening competition, predation may prevent competitive exclusion, as is suggested by the theory of predator-mediated coexistence. It then becomes interesting to ask questions about the frequency, spatial pattern, and predictability of predation events, like those asked about abiotic physical disturbances. Our meta-analysis cannot address these types of questions, but it shows how consistently important predation can be as a factor that diminishes competitive interactions in the field.

Predation should not necessarily always relax the intensity of competition, however. Theoretical models have predicted a variety of different effects of predators on competition among organisms at a lower trophic level,

depending on the nature of the predation and the assumptions of the models (e.g., Armstrong 1979; Oksanen 1992; Holt et al. 1994; Hambäck 1998). The results will vary depending on, for example, whether or not the preferred prey is the dominant competitor, whether or not optimal foraging is incorporated in the model, and whether or not consumption is seasonal or nonseasonal. Because the experiments reported here were generally restricted in scale, were of short duration, and often used enclosures or exclosures, it might perhaps be surprising that the results were as clear as they were. It would be difficult to say, however, that they definitively confirm or refute the predictions of any particular model.

Partitioning the meta-analysis by competition-response variable and also by trophic group, as the data allowed, showed how the general conclusions about the interaction between competition and predation were not equally applicable to all variables and groups. Some findings departed from the overall pattern of competitor removal having small to moderate positive effects that were intensified when predators were removed. In particular, we found two results for competition measured as survival that seem counterintuitive but which might actually make sense. First, for anurans, competitor removal had a negative effect on survival of the focal organisms when predators were present and a positive effect on survival only

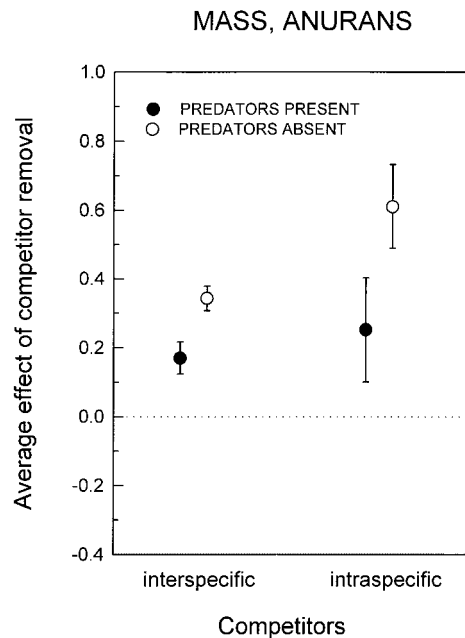


Figure 7: Average effect sizes, d_{+} or d_{p+} , of competitor removal on the individual mass of anurans (95% confidence intervals) in the presence (closed circles) and absence (open circles) of predators. Results are shown separately for interspecific and intraspecific competition.

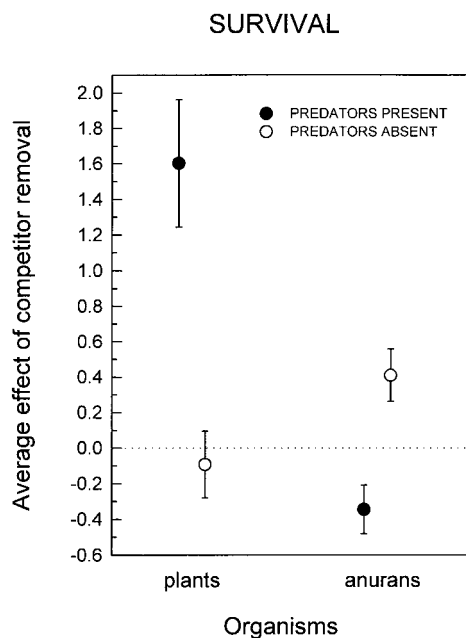


Figure 8: Average effect sizes, d_{++} or d_{p++} , of competitor removal on organisms' survival (95% confidence intervals) in the presence (closed circles) and absence (open circles) of predators. Results are shown separately for plants and anurans.

when predators were removed (fig. 8). It seems plausible that the survival of the focal anurans was higher because their competitors were diverting some of the predation pressure from them. This appears to contradict the idea of competition for enemy-free space, whereby the presence of competitors attracts more shared predators, thus reducing the survival of both competitor species (e.g., Schmitt 1987). These anuran experiments were carried out in enclosures, with predators either added or excluded experimentally, so they may show a different pattern than if predators were allowed to colonize naturally. The effect of predator removal on competition will also depend on which competitor is the preferred prey (e.g., McPeck 1998). Clearly, there are important differences like these among studies that may be important but that could not be grouped for comparison in this meta-analysis because of the small number of appropriate studies. This remains a challenge for the future. Nevertheless, competition resulted in surviving anurans growing less and being smaller, and these competitive effects were more severe when predators were absent (figs. 5, 7). Thus, for anurans, the interaction of predation with competition is even more influential than the general result suggests. Not only does predation lessen the effect of competition during growth, it also makes competition beneficial for the survival of competing prey individuals. So, the interaction of pre-

dation and competition may act in two ways to promote diverse anuran communities.

The other finding for survival that may seem puzzling at first is that the direction of the interaction for plants is opposite that for other organisms. Plants suffered more from competition in the presence of herbivores than in their absence (fig. 8). While this result is based on a small number of studies, it might be reasonable to expect that a plant experiencing both competition and herbivory might suffer greater mortality than a plant experiencing competition alone. In this case, herbivory would act to reinforce the outcome of competition and lessen the chances for coexistence, with those species that are good competitors even more likely to dominate the community. Of course, this idea assumes that the focal organism in the study that is experiencing competitor removal is also the primary target of the herbivore. Our expectation would change if the herbivore more readily attacks the competitor species. In that case, herbivory would act as predation does in most of the other studies—in the presence of herbivory, the intensity of competition would be reduced, allowing coexistence (Pacala and Crawley 1992). In the studies included here, plants suffered modest competitive effects on growth that did not change when herbivores were excluded (fig. 5; note that competitive effects on plant growth were not significantly different from 0, as indicated by the CIs). Current perspectives on the effects of herbivores on plant

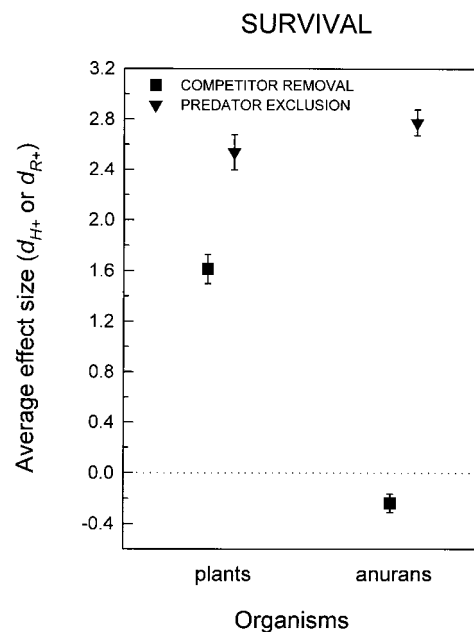


Figure 9: Overall average effect sizes of competitor removal, d_{R+} (square symbols), and predator exclusion, d_{H+} (triangles), on survival for plants and anurans (95% confidence intervals).

communities and trophic webs suggest that these effects can sometimes be profound (e.g., Huntly 1991; Persson 1999). Many more field experiments of this type are needed if we are to be able to adequately generalize about how competition and herbivory interact and how this interaction affects natural plant communities.

In addition to the interaction effects discussed above, the meta-analysis also allowed us to assess the overall effects of predation and competition as main factors and, therefore, allowed us to address predictions 2 and 3 on the relative magnitude of these effects. The results varied among response variables and organism types, so we cannot draw a single universal conclusion in comparing the intensity of competition and predation to support either strictly top-down or bottom-up control of trophic structures. Predation had very large negative effects on survival, on average, while competition had more modest effects; predation is clearly more deadly than is resource competition. Competitor removal had moderate positive effects, on average, on growth and mass, while the effects of predator removal on growth and mass varied among organisms, with moderate positive effects on plants and carnivores but negative effects on anurans (figs. 4, 6). So, based on these findings for survival, growth, and mass, both competition and predation may influence the development of trophic structures, although they do so at different stages. Top-down effects of predators on lower trophic levels clearly have much greater influence on survival than do those of competitors; so, at the most basic level—who survives and who does not—the top-down influence is paramount. Still, competition does influence survival (survival is greater when competitors are removed, fig. 4), so a bottom-up component of control over who survives to be included in a trophic level also exists. But surviving individuals must also grow and acquire mass in order to continue to survive and reproduce. Both competition and predation have major effects on these fitness components.

However, much of the theory and debate about top-down or bottom-up control of food webs largely concerns effects on population densities, and the data on mass, growth, and survival apply to the performance of individual organisms. The experimental evidence suggests that, on average, the effects of competition and predation on organisms' densities were both substantial and did not differ significantly from one another. At a very basic level, our conclusions agreed with some of those of Sih et al. (1985); they reported that competition and predation were both generally important in field experiments. Also in agreement with these authors, we found that the effects of herbivory were larger than those of competition among plants, at least on survival (fig. 9). We found, however, that competition and herbivory had equivalent modest

effects on plant growth (fig. 6). But most of our conclusions cannot be directly compared with those of Sih et al. (1985) both because we had access to a substantial amount of data that was published after their article came out and also because they used an inadequate (because it does not provide accurate estimates of the magnitude, variation, or heterogeneity in effects) and biased technique (vote-counting) to make quantitative comparisons. Most importantly, the articles reviewed by Sih et al. (1985) did not include sufficient data to analyze the interaction between competition and predation, which was a major focus of our study.

Sih et al. (1985) were not able to compare the magnitude of competitive effects with predation effects, as we did, but only to compare the number of articles reporting statistically significant effects (or the number of articles reporting statistically significant "large" effects). But statistical significance depends on sample size as well as the magnitude of the effect, so the number of articles reporting statistical significance is a poor indicator of the magnitude, frequency, or importance of that effect. Even if the statistical power in each of the studies was identical (and it almost certainly varies by orders of magnitude among studies), the number of articles reporting an effect does not say anything about whether that effect is large or small. In addition, vote-counting does not provide any reliable way of comparing the magnitude of the responses among different types of organisms. By using meta-analysis techniques for data synthesis, we were able to make detailed comparisons of both the magnitude of the responses to competition and predation and to compare statistically the responses of different types of organisms. Sih et al. (1985) distinguished between individual-level and higher-level responses to predation but did not further distinguish individual responses. We found this to be important in our analysis; for example, effects of these factors on survival were quite different than effects on growth.

The validity of the findings of meta-analyses have been debated based on a number of issues (e.g., see Cooper and Hedges 1994). Critics have expressed concern, among other things, for the effects of publication bias (the possibility that significant results may be more likely to be published, while nonsignificant results cause studies to languish unpublished in file drawers) on the conclusions (Begg 1994). This is always a possibility, but publication bias may or may not be a particularly severe problem for our synthesis. The focus of many of the primary studies we used here was not the same as the focus of the research synthesis, and so it is reasonable to surmise that the findings we were looking for in these studies did not necessarily have a large effect on their likelihood of being published. We were particularly interested in the relationship between competition and predation. While studies that showed no

effect of either competition or predation might conceivably remain unpublished, it seems unlikely that sufficiently strong or consistent biases exist regarding their relative magnitudes and interaction to deny publication in any predictable fashion. Further, publication bias, if it exists, will also affect any other attempt to generalize from or make sense of the results of published experiments, no less than it affects formal data synthesis techniques (i.e., meta-analysis), and so is not a problem unique to quantitative approaches to generalization.

Of much more potential concern here is the problem of research bias, the propensity to study certain organisms and systems much more heavily than others, sometimes with the expectation of finding significant results (Gurevitch and Hedges 1999). This problem is not unique to this study but is common to most ecological research synthesis, whether based on traditional narrative approaches or more quantitative techniques such as meta-analysis. Research bias is likely in the collection of studies we assembled. As a consequence, we would advise a cautious interpretation of our conclusions: while we are confident that they are a reliable summary of the available evidence, the available evidence omits many important organisms and systems. The only way to improve our knowledge is to increase our knowledge base by bringing more experimental evidence to bear on this question.

Competition and predation are often assumed to be among the most important biotic factors affecting plant and animal populations. Evidence from field studies in which both factors were experimentally manipulated confirms that this appears to be a fair assumption and also confirms that these factors commonly interact with one another. Our understanding of the importance of the interaction between these factors in nature would benefit greatly from expanding the number of experiments done, the range of organisms on which these questions have been investigated, and particularly by increasing the number of studies that focus on population-level parameters (e.g., density) rather than on individual performance (Goldberg and Barton 1992).

In addition, experimental evidence in ecology has been faulted for being small in scale and of short duration. Additionally, Hassell et al. (1998) emphasize the impor-

tance of distinguishing between how top-down or bottom-up processes may influence populations versus how they may regulate populations. The measurements made in our collection of studies only address the influence of competition and predation, so extrapolating from these experimental results to natural food webs must therefore be done with some caution. Experimentalists who focus exclusively on competition or on herbivory and predation may need to consider potential interactions with the other factors in assessing the magnitude and importance of either one. Generally, competition studies do not specify predation or herbivory levels, and, similarly, predation studies may not consider the effects of modifying competition. However, while it is easy to call for longer, bigger, more complex field experiments, this is not only difficult and expensive but also raises a host of new problems and difficulties. We believe strongly that the available experimental evidence is, despite its limitations, a mine of information on the responses of organisms in natural or seminatural systems.

Ecology is an inherently factorial science. The task of extracting general principles from a growing collection of necessarily complex studies requires sound quantitative methods to synthesize factorial data. Our use of factorial meta-analysis to survey field experiments that manipulated both competition and predation is one example of the potential value of this technique to ecology. How easily this potential is reached, however, will depend in part on raising standards for data reporting (Gurevitch et al. 1992). This is a fundamental requirement for our science as we move into an era in which meta-analysis informs general conclusions to an increasing extent.

Acknowledgments

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APPENDIX

Calculations Involved in the Factorial Meta-Analysis

The first step in carrying out the meta-analysis was to calculate a standardized measure from each of the individual experiments of the effect of competitor removal when predators were absent (d_a):

$$d_a = \frac{(\bar{Y}_{ae} - \bar{Y}_{ac})}{s} J(m),$$

as well as its effect when predators were present (d_p):

$$d_p = \frac{(\bar{Y}_{pe} - \bar{Y}_{pc})}{s} J(m).$$

Subscripts indicate that predators are present (p) or absent (a) and that competitors are at natural ("control") density (c) or experimentally reduced density (e). The expression \bar{Y} is the mean performance of the group indicated by the subscript; s is the pooled standard deviation of the two groups; $J(m)$ is a correction term for small sample bias (Hedges and Olkin 1985). Therefore, a positive value for d_a or d_p indicates a positive response to the removal of competitors in the absence or presence, respectively, of predators. In those cases where competitors were experimentally enhanced rather than reduced, effect sizes were calculated in the same way as were experimental reductions, but the sign of the mean for the competitor manipulation group (Y_{ae} or Y_{pe}) was reversed to make the organisms' responses comparable to those in other experiments. The denominator, s , is the pooled sampling variance across all four treatment groups:

$$s = \sqrt{\frac{(N_{pe} - 1)(s_{pe})^2 + (N_{pc} - 1)(s_{pc})^2 + (N_{ae} - 1)(s_{ae})^2 + (N_{ac} - 1)(s_{ac})^2}{N_{pe} + N_{pc} + N_{ae} + N_{ac} - 4}},$$

where N is the sample size (number of individuals) and s_{ij} is the standard deviation of the mean at each treatment level (as indicated by the subscripts) in that study.

The overall effect of predator (or herbivore) exclusion, d_H , can be calculated for each study by pooling across the two competitor manipulation levels to compare the difference between the means of groups where predators were present and where they were absent:

$$d_H = \frac{(\bar{Y}_{ae} + \bar{Y}_{ac}) - (\bar{Y}_{pe} + \bar{Y}_{pc})}{2s} J(m),$$

where s is the pooled standard deviation, as above. A positive value for d_H , therefore, indicates that there was a positive response to the exclusion of predators (across competition treatments).

Analogously, we calculate the overall effect of competitor removal in each study, d_R , by pooling across the two predation treatments to compare the difference between the means of groups where competitors were present and where they were removed:

$$d_R = \frac{(\bar{Y}_{ae} + \bar{Y}_{pe}) - (\bar{Y}_{ac} + \bar{Y}_{pc})}{2s} J(m).$$

A positive value for d_R demonstrates a positive response to the removal of competitors (across predation treatments);

that is, a positive d_R is evidence of competition. In addition to calculating d_H and d_R for the main effects of predator exclusion and competitor removal, we can calculate an interaction effect size, d_I , as a measure of the magnitude of the interaction between the two factors in each experiment:

$$d_I = \frac{(\bar{Y}_{ae} - \bar{Y}_{ac}) - (\bar{Y}_{pe} - \bar{Y}_{pc})}{s} J(m).$$

A positive value of d_I shows that competitor removal in the absence of predators has a greater effect than in the presence of predators; that is, competition is more intense when predators are excluded than when they are present.

Once effect sizes have been calculated for each study, we may proceed to conduct the meta-analysis. To combine the results across studies, the effect sizes are weighted by the inverse of their sampling variances for calculating mean effect sizes and conducting statistical tests. The sampling variances for d_a for each study are calculated as they would be in any two-factor meta-analysis (e.g., Gurevitch and Hedges 1993):

$$\hat{s}^2(d_a) = \frac{N_{ae} + N_{ac}}{(N_{ae}N_{ac})} + \frac{d_a^2}{2(N_{ae} + N_{ac})} = \frac{1}{N_{ae}} + \frac{1}{N_{ac}} + \frac{d_a^2}{2(N_{ae} + N_{ac})}$$

or, analogously, for d_p . The sampling variance of d_H is

$$\hat{s}^2(d_H) = \left[\frac{1}{N_{pe}} + \frac{1}{N_{pc}} + \frac{1}{N_{ae}} + \frac{1}{N_{ac}} + \frac{d_H^2}{2(N_{pe} + N_{pc} + N_{ae} + N_{ac})} \right] \frac{1}{4},$$

and, for d_R ,

$$\hat{s}^2(d_R) = \left[\frac{1}{N_{pe}} + \frac{1}{N_{pc}} + \frac{1}{N_{ae}} + \frac{1}{N_{ac}} + \frac{d_R^2}{2(N_{pe} + N_{pc} + N_{ae} + N_{ac})} \right] \frac{1}{4}.$$

The interaction variance is calculated as

$$\hat{s}^2(d_I) = \frac{1}{N_{pe}} + \frac{1}{N_{pc}} + \frac{1}{N_{ae}} + \frac{1}{N_{ac}} + \frac{d_I^2}{2(N_{pe} + N_{pc} + N_{ae} + N_{ac})}.$$

Using the inverse of the sampling variances above as weights (Gurevitch and Hedges 1993), we calculated the average mean weighted effect sizes of competition with predators excluded or present, d_{a+} or d_{p+} , the average main effect of predator exclusion, d_{H+} , the average main effect of competitor removal, d_{R+} , and the interaction effect (d_{I+}) between the two factors (predator exclusion and competitor removal).

The degrees of freedom, m , in calculating the correction factor (Hedges and Olkin 1985; Gurevitch and Hedges 1993) are calculated conventionally; that is, $m = N_{ae} + N_{ac} - 2$ for d_a , and $m = N_{ae} + N_{ac} - 2$ for d_p , except for calculating the average effects of competition and predation and the interaction term between competition and predation, where the degrees of freedom are $m = N_{pe} + N_{pc} + N_{ae} + N_{ac} - 4$, since four treatment groups are used in these calculations.

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