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## PREDATOR DIVERSITY AND TROPHIC INTERACTIONS

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**Abstract.** The recognition that predators play important roles in ecosystems has prompted research to resolve how combinations of predator species influence ecosystem functions. Interactions among predator species and their prey can lead to a host of linear and nonlinear effects. Understanding the conditions causing these effects is critical for assigning predator species to functional groups in ways that lead to predictive theory of predator diversity effects on trophic interactions. To this end, I provide a synthesis of experiments examining multiple-predator-species effects on mortality of single shared prey. I show how experimental design and experimental venue can determine the conclusion about the importance of predator diversity on trophic interactions. In addition, I link natural history insights on predator species habitat and hunting behavior with linear and nonlinear multiple-predator effects to derive a new concept of predator diversity effects on trophic interactions. This concept holds that the nature of predator diversity effects is contingent upon predator species hunting mode plus predator and prey species habitat domain (defined as the spatial extent to which a microhabitat is used by a species). This concept allows the classification of multiple-predator effects into four broad functional categories: substitutable, nonlinear due to predator species interference, nonlinear due to intraguild predation, and nonlinear due to predator species synergism. Experimental evidence so far provides ample and comparatively equal support for substitutable, interference, and intraguild effects, and equivocal support for nonlinear synergisms. The paper closes by discussing ways to further a research program aimed at using the building blocks presented here to understand predator functional diversity and trophic interactions in complex ecological systems.

**Key words:** *habitat domain; hunting mode; intraguild predation; multiple predators; predator and prey traits; predator diversity; risk enhancement and reduction; trophic interactions.*

### INTRODUCTION

Predation and competition are primary determinants of the structure and functioning of ecological systems (Holt and Polis 1997, Sih et al. 1998). In as much as these interactions involve myriad kinds of species, then a logical deduction is that the level of ecological function must somehow be related not only to the diversity of species within a system, but to the variety of ways that species participate in these interactions. Accordingly, a major thrust of contemporary ecology is to discern the mechanistic links among species diversity, species interactions, and levels of ecological function (Hooper et al. 2005). In this endeavor, ecologists are confronted

with two important issues: one conceptual; the other technical.

Ecosystem functions depend not on the diversity of species per se but on the diversity of functional characteristics of organisms present in the ecosystem (Hooper et al. 2005). The important conceptual issue here is developing meaningful characterizations of species' functional roles (Duffy 2002, Chalcraft and Reserits 2003, Hooper et al. 2005, Petchey and Gaston 2006, Wright et al. 2006). But the functional role of a particular species may depend upon the kinds of species with which it is interacting (Duffy 2002, Hooper et al. 2005). Explaining such context dependency may then be the single most important hurdle to overcome in developing predictive theories of species diversity and ecosystem function. Developing predictive theory also requires knowing the causal linkages between the focal components of a system and system function, which brings us to the second, technical issue. Ecologists use

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experiments to gain cause–effect insights because they provide control over extraneous variables, and through replication they can lead to reasonably precise insights (Hairston 1990). But experiments are contrivances and therefore careful attention must be paid to carry out experiments in ways that provide realistic insights rather than experimental artifacts (Loreau and Hector 2001, Skelly 2002, Fox 2005).

This paper deals with both issues to develop a framework for understanding how functional characteristics of predators influence the nature of predator diversity effects in ecosystems and to encourage research that tests predictions of this framework. Understanding predator diversity effects is becoming an increasingly important avenue of ecological research. Predators can offer important ecosystem services by directly controlling the abundances of herbivores that are potentially agricultural pests (Hochberg 1996, Symondson et al. 2002, Ives et al. 2005, Snyder et al. 2005, Tscharrntke et al. 2005), and by indirectly affecting ecosystem functions such as primary productivity and elemental cycling (e.g., Downing and Leibold 2002, Paine 2002, Duffy 2003, Duffy et al. 2005, Fukami et al. 2006, Maron et al. 2006, Schmitz 2006).

Ecologists have traditionally downplayed predator diversity effects by assuming predators can be treated collectively as a single, distinct trophic level (Fretwell 1987). This necessarily assumes that predator species have identical effects in ecosystems and are thus functionally substitutable (Chalcraft and Resetarits 2003). Such a conceptualization has been roundly critiqued because it often does not accord with ecological reality (see reviews by Polis and Strong 1996, Sih et al. 1998, Duffy 2002, Ives et al. 2005). Predator species can interact synergistically or antagonistically, and such nonlinear effects can enhance or weaken their collective effect on ecosystem structure and functioning.

The emergence of nonlinear effects has been variously attributed to predator species morphological traits, microhabitat use, and foraging behavior, and to the phenotypic responses of prey to specific predator species (Schoener 1971, Huey and Pianka 1981, Sih et al. 1998, Chalcraft and Resetarits 2003, DeWitt and Langerhans 2003, Relyea 2003, Rosenheim et al. 2004, Denno et al. 2005, Ives et al. 2005, Schmitz 2005). Yet much recent theory addressing predator diversity effects in ecosystems (e.g., Thébault and Loreau 2003, 2006, Fox 2004, Ives et al. 2005, Casula et al. 2006) has not explicitly incorporated this biological detail. This may stem in part from an empirical research program that has generated a vast collection of case studies (e.g., Sih et al. 1998: Table 1) but provided little if any synthetic insights that allow one to predict when a particular kind of linear or nonlinear effect should arise.

My goal here is to provide the conceptual building blocks needed to construct theory that predicts occurrences of linear and nonlinear predator diversity effects

in ecosystems. This goal is reached via three parts: background, empirical synthesis, and concept development. The background section helps to organize the empirical synthesis by addressing important technical issues related to experimentation and by offering conceptual background on predator functional characteristics. I address how different experimental designs may lead to different conclusions about the importance of predator diversity in ecological systems, how experimental design can introduce confounding factors that lead to faulty inferences, and how to control for confounding factors when making inferences. I also introduce two predator functional characteristics (hunting mode and habitat domain) that together can explain the nature of single predator–prey interactions. The technical and conceptual information is then used to steer data extraction in the empirical synthesis of the ecological literature. The synthesis reveals how experimental design and experimental venue (field vs. laboratory) indeed lead to different conclusions about multiple-predator effects, and suggests which conclusions might be suspect. It also reveals pattern in the way predator functional characteristics cause linear and nonlinear predator diversity effects. The final section builds on the synthesis by developing the conceptual framework for classifying functional roles of predator species. This framework produces testable predictions about the way hunting mode plus habitat domain affect the nature of predator diversity effects on prey. The paper closes by elaborating on the kind of research program that is needed to provide quantitative, mechanistic tests of the conceptual framework.

#### BACKGROUND: LINKING THEORY TO EXPERIMENTAL DESIGN

Experimental ecologists take a decidedly statistical perspective when choosing an experimental design to test for predator diversity effects (Soluk and Collins 1988, Wilbur 1997, Sih et al. 1998). The typical focus is on the factorial nature of a study and appropriate tests for linearity (and alternatively nonlinearity) of predator diversity effects (Sih et al. 1998). But there are two kinds of linearity that must be considered, and, as shown using the following ecological perspective, they lead to different inferences about links between predator diversity and function.

The interaction between a prey species and  $n$  predator species can be specified generically using a dynamical systems model of the following form:

$$\begin{aligned} dN/dt &= Nf(N) - \rho(P_1, P_2, \dots, P_n)N \\ dP_i/dt &= g(N)P_i \quad i = 1, 2, \dots, n \end{aligned} \quad (1)$$

where  $N$  and  $P_i$  are the population densities of the prey and predator species  $i$ , respectively,  $f(N)$  is a function describing per capita prey growth rate in relation to prey density,  $\rho(P_1, P_2, \dots, P_n)$  is a function describing the collective net effect of all predator species in the system on

TABLE 1. Outcome of experimental studies examining predator diversity effects on a common prey. Studies are categorized by design (additive vs. replacement series) and by venue (laboratory or field).

Experimental design and outcome	Source	Venue
<b>Additive experimental design</b>		
Risk enhancement	Sih et al. (1998)	laboratory (five studies)
	Losey and Denno (1998)	laboratory/field
	Nyström et al. (2001)	field
	Cardinale et al. (2003)	field
Risk reduction	Sih et al. (1998)	laboratory (eight studies)
	Crumrine and Crowley (2003)	laboratory
	Warfe and Barmuta (2004)	laboratory
	Finke and Denno (2005)	laboratory
	Sih et al. (1998)	field (five studies)
	Vance-Clacraft et al. (2005)	field
	Griffen (2006)	field
Linear-additive	Sih et al. (1998)	laboratory (eight studies)
	Björkman and Liman (2005)	laboratory
	Fairchild and Holomuzki (2005)	laboratory
	Finke and Denno (2005)	laboratory
	Griswold and Lounibos (2006)	laboratory
Linear-substitutable	Aukema et al. (2004)	laboratory
<b>Replacement series experimental design</b>		
Risk enhancement	Aquilino et al. (2005)	laboratory
	Bruno and O'Connor (2005)	laboratory
	Wilby et al. (2005)	laboratory
	Snyder et al. (2006)	laboratory
	Van Son and Thiel (2006)	laboratory
	Griffen (2006)	field
Risk reduction	Sih et al. (1998)	laboratory (two studies)
	Lang (2003)	field
	Siddon and Witman (2004)	field
	Vance-Clacraft et al. (2005)	field
	Aquilino et al. (2005)	laboratory
Linear-substitutable	Bruno and O'Connor (2005)	laboratory
	Wilby et al. (2005)	laboratory
	Byrnes et al. (2006)	laboratory
	Sokol-Hessner and Schmitz (2002)	field
	Straub and Snyder (2006)	field
	Griffen (2006)	field

per capita prey population growth rate, and  $g(N)$  is a function describing the conversion of prey consumed into per capita population growth rate of predator species  $i$ .

In this formalism one can express multiple-predator effects on a common prey in at least two ways. First, one could treat all individuals of all predator species as though they were  $m$  individual members of a single functional “species” or functional group. The term describing the net effect of these predators on per capita prey population growth rate is derived by taking the average of the effects of  $m$  individual predators of that “species” population where

$$\rho(P_i, P_j, \dots, P_n) = \alpha P = \sum_{k=1}^m \alpha_k P_k / m. \quad (2)$$

Alternatively, one could treat the predator species as  $n$  separate populations. The term accounting for the net effect of these predator species on per capita prey population growth rate can be derived by adding the contribution of each predator species  $i$  where

$$\rho(P_i, P_j, \dots, P_n) = \sum_{i=1}^n \alpha_i P_i. \quad (3)$$

In both terms, the effects of predator species combine linearly. But, in Eq. 2, linearity arises because predators are assumed to have substitutable effects on the prey species. Such linearity is detected experimentally using the replacement (substitutive) series design (Sih et al. 1998). In Eq. 3 total predator density increases with the number of predator species added (i.e., predator density and predator species diversity covary). Such linearity is detected experimentally using an additive design (Sih et al. 1998). Replacement series experiments can lead to the conclusion that predator diversity and function are unrelated because the predator species are functionally redundant; additive experiments can lead to the conclusion that predator diversity and function are related because predator species complement each other. Thus it is possible to draw altogether different conclusions about the functional role of an identical set of predator species simply as a consequence of the way the predator species are combined experimentally (e.g., see Griffen 2006)—an experimental artifact.

Additive experiments have also revealed two kinds of nonlinear effects. Multiple predators may have risk-enhancing effects (Sih et al. 1998), a synergism, if prey experience higher mortality in multiple-predator systems

than would be expected based on the sum of mortalities in single-predator systems. Alternatively, multiple predators may have risk-reducing effects whenever prey have lower mortality in multiple-predator systems than would be expected based on the sum of mortalities in single-predator systems (Sih et al. 1998)—an antagonism. With risk enhancement, predator species diversity and function are positively related. With risk reduction, predator species diversity and function are negatively related. Thus, additive designs have a high likelihood of producing a conclusion that there is some relationship between predator species diversity and function. But this may stem from the fact that additive experiments confound predator density and diversity.

This situation argues for a systematic approach that guards against the likelihood of falsely concluding that predator diversity and function are related. I submit that such an approach should begin by testing a null conception that predator diversity and function are unrelated, implying the use of replacement series designs. Yet the number and density of predator species covary positively in many systems. It makes sense, then, to deploy additive designs to understand natural system functioning. But one must then address the confounding effects of density on diversity.

#### *Test condition for substitutability in additive experiments*

Finke and Denno (2005) proposed that the effect of density in additive designs can be factored out by calculating a per capita effect magnitude for each experimental treatment. Effect magnitude is first calculated as the log ratio  $\ln(N_t/N_c)$ , where  $N_t$  is the prey response variable (final prey density or prey mortality rate) in the predator species treatment and  $N_c$  is the prey response variable in the control (Osenberg et al. 1997, Wootton 1997). Per capita effect magnitude is then calculated by dividing each effect magnitude estimate by the predator density for the respective paired treatment–control (Finke and Denno 2005). They do not, however, provide an explicit test condition for substitutability using these metrics.

In an additive design,  $n$  predator species will be substitutable if the effect magnitudes satisfy the following condition (derived in Appendix A):

$$\sum_{i=1}^n (R_i/P_i) = nR_{1+2\dots+n} \left/ \sum_{i=1}^n P_i \right. \quad (4)$$

where  $R_i$  is the log ratio effect magnitude of predator species  $i$  in a single-predator treatment,  $P_i$  is the density of predator species  $i$  in the single-predator treatment, and  $R_{1+2\dots+n}$  is the log ratio effect magnitude of the multiple-predator treatment. I use this test condition below (*Synthesis: Predator diversity effects*) to determine if the conclusions from studies using additive designs are upheld once the confounding effects or predator density are taken into account.

#### *Linking predator characteristics to the nature of predator diversity effects*

Sih et al. (1998) showed that there are three broad kinds of multiple-predator effects: linear (substitutable and additive), risk-enhancing, and risk-reducing. The challenge in developing a predictive theory is to explain the ecological conditions that lead to these outcomes. One productive way to begin meeting this challenge is to distill several critical components of the natural history and traits of predators and prey (Schoener 1971, Huey and Pianka 1981, Sih et al. 1998, Chalcraft and Reseterits 2003, DeWitt and Langerhans 2003, Relyea 2003, Rosenheim et al. 2004, Warfe and Barmuta 2004, Denno et al. 2005, Ives et al. 2005) into two variables, predator hunting mode plus predator and prey habitat domain, that have been shown to determine the outcome of single-predator single-prey interactions (Schmitz 2005).

This approach expands upon earlier ideas (Schoener 1971, Huey and Pianka 1981, Sih et al. 1998) by classifying predators according to three hunting modes. The three hunting modes are (Schmitz 2005): (1) sit-and-wait, in which an ambush predator remains at a fixed location for prolonged periods whether it is hunting or not (days to weeks); (2) sit-and-pursue, where the predator remains at a fixed feeding location and rushes at and pounces on prey when they are in the predator's vicinity. These predators move to new feeding locations once prey become scarce; and (3) active, where predators are continuously on the prowl seeking prey. This discrete classification scheme is intended to motivate thinking about predator functional roles. I deal with biologically more realistic cases of flexibility among hunting modes in *Concept: Advancing a research program on predator diversity effects* later in the article.

I also examine habitat use by advancing the concept of habitat domain (Schmitz 2005). Habitat domain differs from conventional definitions of habitat use (e.g., microhabitat choice) by considering both microhabitat choice and the extent of spatial movement within the chosen microhabitat. This idea (Schmitz 2005) was motivated by observations of three predator species in an old-field system in which microhabitat can be defined crudely as patches of grass and herbs (Schmitz and Suttle 2001). All three predators use both grass and herb patches. But this is not a complete description of microhabitat use, because the three predators are spatially segregated. One species resides in the upper canopy, one species ranges throughout the middle canopy, and one species occupies the lower canopy and ground (Fig. 1). The predator that roams freely throughout the entire grass and herb microhabitat has a broad habitat domain (Fig. 1). The predator species that use only a portion of the microhabitat (e.g., upper canopy leaves and flower heads, or lower canopy and ground) have a narrow habitat domain (Fig. 1). In the next section, I show how hunting mode and habitat domain are useful for organizing natural history

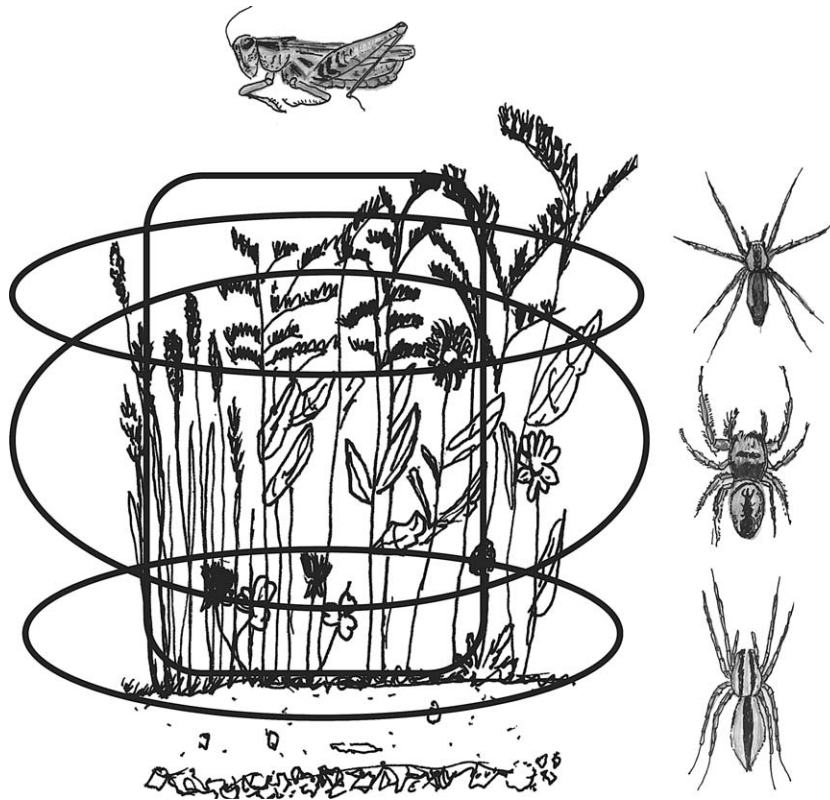


FIG. 1. The figure illustrates the habitat domain concept, where habitat domain is defined as the spatial extent to which a microhabitat is used by a species. Prey habitat domain is depicted as a vertical rectangle; predator habitat domain is depicted as horizontal ellipses. Microhabitat is defined as the collection of grass and herb patches. *Melanoplus* grasshoppers use both grass and herbs and move throughout the entire vertical canopy: they have a broad habitat domain. The spiders *Pisaurina* and *Rabidosa* (top and bottom species, respectively) use extended portions of the entire available microhabitat and hence have narrow habitat domains in the upper and lower canopy, respectively. The hunting spider *Phidippus* uses the entire middle-upper canopy and therefore has a broad habitat domain. Grasshoppers overlap completely with all three predators. The predators are segregated vertically and so have spatially complementary habitat domains.

information to identify pattern in the nature of multiple-predator effects.

#### SYNTHESIS: PREDATOR DIVERSITY EFFECTS

##### *Literature search*

My synthesis builds on the 24 studies assembled by Sih et al. (1998). I identified studies postdating Sih et al. (1998) by conducting an electronic search of peer-reviewed publications using the key words: multiple predators; multiple-predator effects; predators and biological control; predator identity; predator identity effects; and predator diversity and ecosystems. I used only studies that met the following criteria. A study had to manipulate two or more predator species and examine their single and combined effects on a focal prey species. Experiments had to allow predator species to interact freely with each other and with their prey (as opposed to presenting cues of predator presence).

The identified studies were grouped according to type of effect, as concluded by the investigator, and by experimental design (Table 1). I found 13 studies that employed additive designs and 13 studies that employed

replacement series designs (Table 1). I listed the experimental venue used in each study (Table 1). Field experiments are defined as studies conducted within plots or enclosure cages containing naturally growing vegetation (microhabitat) in field settings (terrestrial fields, ponds, or streams), or in crops within agricultural fields. Laboratory experiments are defined as studies conducted in artificial ponds and streams, mesocosms at field stations, and microcosms within greenhouses or laboratory buildings into which vegetation (microhabitat) was transplanted.

Field and laboratory experiments used similar numbers (mean  $\pm$  SE) of predator species ( $2.5 \pm 0.18$  species,  $n = 16$ ; compared with  $2.4 \pm 0.05$  species,  $n = 32$ ). But the venue size for the field experiments ( $3.25 \pm 0.98$  m<sup>3</sup>,  $n = 16$ ) was 10 times larger than for laboratory experiments ( $0.288 \pm 0.09$  m<sup>3</sup>,  $n = 32$ ). All study durations were short (days to a couple of months), and thus only measured mortality effects on prey as the demographic variable. Table 1 reveals the full gamut of possible linear and nonlinear outcomes. There were

multiple outcomes in some studies depending on the particular combination of species.

#### *Comparing conclusions from field and laboratory studies*

Laboratory experiments led to the conclusion of risk enhancement in 30% of cases, risk reduction in 30% of cases, and linear effects in 40% of cases. Field experiments revealed risk enhancement in 7% of cases, risk reduction in 71% of cases, and linear effects in 22% of cases. The differences in frequency of the three types of effect between laboratory and field experiments is significant (chi-square test for independence:  $\chi^2 = 7.72$ ,  $df = 2$ ,  $P < 0.01$ ). This implies that laboratory experimentation may have a higher likelihood than field experimentation of concluding that predator diversity enhances function.

#### *Testing for substitutability in additive experiments*

To determine how the confounding effects of predator density and diversity might influence conclusions, I reexamined the additive experiments reported in Sih et al. (1998) and in Table 1. I extracted data from those studies to calculate the effect magnitudes (Eq. 4) needed to test for substitutability (Appendix B). I was able to do this for 60% of the studies. I could not do so for the remaining 40% for reasons ranging from lack of reports of treatment means (e.g., only ANOVA tables reported), no predator-free control included, or lack of reports of predator densities in treatments (Appendix B). I calculated the test condition for each independent combination of predator species and focal prey species. I pooled the estimates for the entire prey base whenever several prey species were combined in single experimental treatments.

In 57% of the studies, the conclusion drawn by the investigator was inconsistent with the conclusion drawn using the test condition for substitutability (Appendix B). Indeed, there was an inconsistency in 100% of the studies concluding risk enhancement, in 45% of the studies concluding risk reduction, and in 57% of the studies concluding linear, additive effects. These results, coupled with experimental evidence that additive and substitutive experiments can lead to different inferences about predator diversity effects (Griffen 2006), argue that conclusions drawn from additive experiments should be treated cautiously if a companion test for substitutability is not provided.

#### *Hunting mode, habitat domain, and the nature of predator diversity effects*

Motivated by the idea that habitat domain and hunting mode may offer clues into the nature of predator diversity effects, I probed deeper into individual studies to obtain natural history detail on the hunting mode and microhabitat use of predator and prey species. I only included experiments listed in Table 1 that were conducted under field conditions because they were less likely to constrain species interactions and

thus create artifacts due to venue size. I examined both replacement series and additive field experiments. I included only those additive designs for which I was able to test for substitutability (Appendix B). If there was a difference between an author's conclusion and my own based on the test condition for substitutability, I used the revised conclusion drawn from the test condition. These criteria led to 13 independent studies that could be categorized by experimental design and by kind of effect. The studies were conducted in freshwater rivers and ponds, old fields and agricultural fields, and intertidal seashores. They included as few as two predators and as many as six (Appendix C). I next elaborate on the natural history of habitat domain and hunting mode from these studies, because herein lay important clues to understanding the link between predator diversity and the resultant effect.

*Replacement series field experiments with substitutable effects.*—Predator species were substitutable when they had different hunting modes, had broad or narrow habitat domains but in complementary spatial locations, and their prey species had a broad habitat domain (Appendix C). For example, actively hunting jumping spiders moved freely throughout the entire old-field vegetation canopy (broad domain), sit-and-pursue wolf spiders occupied the lower canopy and ground (narrow domain), and sit-and-wait hunting spiders occupied the upper canopy (narrow domain) (Fig. 1). Mortality risk imposed by multiple predators on grasshoppers that roamed throughout the canopy (broad domain) was the average of the mortality imposed by each predator species individually (Sokol-Hessner and Schmitz 2002). In an agricultural field, peach aphids that reside throughout the canopy (broad domain) faced three- or four-species treatment combinations of sit-and-wait and actively hunting predator species (Straub and Snyder 2006). Predator species tended to have complementary habitat domains within the vegetation canopy, resulting in mortality risk in multiple-predator treatments that was the average of the risk imposed by each predator species alone.

*Replacement series field experiments with risk-reducing effects.*—Predators had risk-reducing effects when they had completely overlapping habitat domains (Appendix C). Risk reduction arose from intraguild predation and interference competition. In an agricultural field, herbivorous insect taxa with broad habitat domains (ground and entire vegetation canopy) faced two taxa of predators, wolf spiders and carabid ground beetles, that resided on the ground and in the lower canopy (narrow habitat domain). Prey evaded predators by moving higher in the vegetation canopy. Risk reduction arose because the prey could move to enemy-free space and because predators engaged in intraguild predation (Lang 2003). Alternatively, on an ocean algal bed, actively hunting Jonah crabs and lobsters co-occurred with and hunted urchins on the entire bed (Siddon and Witman 2004). Lobsters interfered with crab foraging,

leading to risk reduction for urchins. In a river system, sit-and-pursue dragonflies and dobsonflies occupied the riverbed and hunted mayflies (Vance-Chalcraft et al. 2005). Both species engaged in interference interactions while vying for hunting locations, thereby reducing mayfly mortality risk.

*Replacement series field experiments with risk-enhancing effects.*—Multiple predators enhanced risk in only one experiment (Appendix C). Mussels, being cemented to a single location (narrow habitat domain), had limited recourse to evade actively hunting green crabs and Asian crabs, both of which had overlapping, broad habitat domains. This risk-enhancing effect was, however, contingent upon mussel density (Griffen 2006). At low density, the predator species had substitutive effects. At high density, the predator species had risk-enhancing effects owing to greater foraging effort than in treatments with low prey density (Griffen 2006).

*Additive field experiments with substitutable effects.*—Hurd and Eisenberg (1990) examined the single and combined effects of mantids and wolf spiders on arthropod taxa, including grasshoppers, crickets, and other spiders found broadly throughout the vegetation canopy. The sit-and-wait mantid's habitat domain, in the mid-canopy, was complementary to the sit-and-pursue spider's habitat domain, which encompassed the lower canopy and the ground (Appendix C). According to the test condition (Appendix B), the multiple-predator effect was the average of the individual species effects. Losey and Denno (1998) showed that in alfalfa fields lady beetles reside in the vegetation canopy and prey on pea aphids there. The pea aphids drop to the ground to evade lady beetles, which makes them vulnerable to predation by *Harpalus* or *Philonthus* ground beetles. This has been regarded as a classic case of risk enhancement. However, the test condition for substitutability (Appendix B) suggests again that these species have substitutable effects.

*Additive field experiments with risk-reducing effects.*—Predators had risk-reducing effects due to interspecific interference (Appendix C). In a saltmarsh system, actively hunting lady beetles and parasitoids preyed on aphids (Ferguson and Stiling 1996). All three species had narrow, completely overlapping habitat domains along selected host plant branches. These conditions led to less mortality risk for the aphid when the two enemies were combined than when they were alone. In the rocky beach system (Griffen 2006) described above, risk reduction arose as a consequence of heightened interspecific interference between predators at high prey densities.

*Additive field experiments with risk-enhancing effects.*—Predators are claimed to have risk-enhancing effects in two additive field experiments (Appendix C). In an experimental pond system, crayfish and trout were stocked with several prey species including tadpoles, snails, and mayflies (Nyström et al. 2001). Trout were effective predators of tadpoles but not of snails and

mayflies. Crayfish were opposite in effectiveness. But this system is effectively two independent food chains rather than a multiple-predator system, because trout did not prey on snails and mayflies, and crayfish did not prey on tadpoles. Thus, even though the combined effect of both predators was greater than the mean of the individual species effects, it is a trivial effect (Fauth 1990, Sih et al. 1998). This is because minor increases in mortality levels in multiple-predator treatments would be considered infinite risk enhancement, since one of the two predator species in a treatment always has no significant direct effect on prey mortality. In an alfalfa field, pea aphids faced damselbugs, ground beetles, and parasitoid wasps that had complementary habitat domains and hunting modes (Cardinale et al. 2003). In this case, the density of an alternative prey species, the cowpea aphid, influenced the likelihood that the parasitoid would attack the pea aphid. In turn, the ground beetle reduced cowpea aphid density, leading to a dramatic host switch by the parasitoid from the cowpea aphid to the pea aphid (Cardinale et al. 2003). Thus, risk enhancement was not strictly due to a multiple-predator effect on a single prey species.

The empirical synthesis suggests that predator species with identical characteristics (i.e., completely overlapping habitat domains and identical hunting modes), intuitively the most likely candidates for functional substitutability, tended to cause risk-reducing effects on their prey via interference or intraguild interactions. Risk enhancement was also detected. But factors other than just predator species diversity caused the effect. Functional substitutability was found whenever prey had broad habitat domains and predators had spatially complementary habitat domains. This last empirical finding seems counterintuitive. But when predators have complementary habitat domains and prey have broad domains, predators are substitutable because replacing one predator species with another simply changes the spatial location in which prey mortality occurs.

#### CONCEPT: PREDATOR DIVERSITY EFFECTS ON TROPHIC INTERACTIONS

The empirical synthesis leads to the working hypothesis that multiple-predator effects are contingent upon two functional characteristics of predator species, hunting mode and habitat domain, and one of prey species, habitat domain. In the following, I predict how these functional characteristics should lead to different kinds of predator diversity effects.

*Substitutability.*—Predator species should have substitutable effects on common prey species whenever they have spatially complementary habitat domains and the prey species have broad habitat domains (Fig. 2a). This arises because there is little if any opportunity for predators to engage in interspecific interactions. Moreover, by roaming freely throughout the canopy, the prey species effectively average across the different predator species. Thus, from the prey species' perspective, a

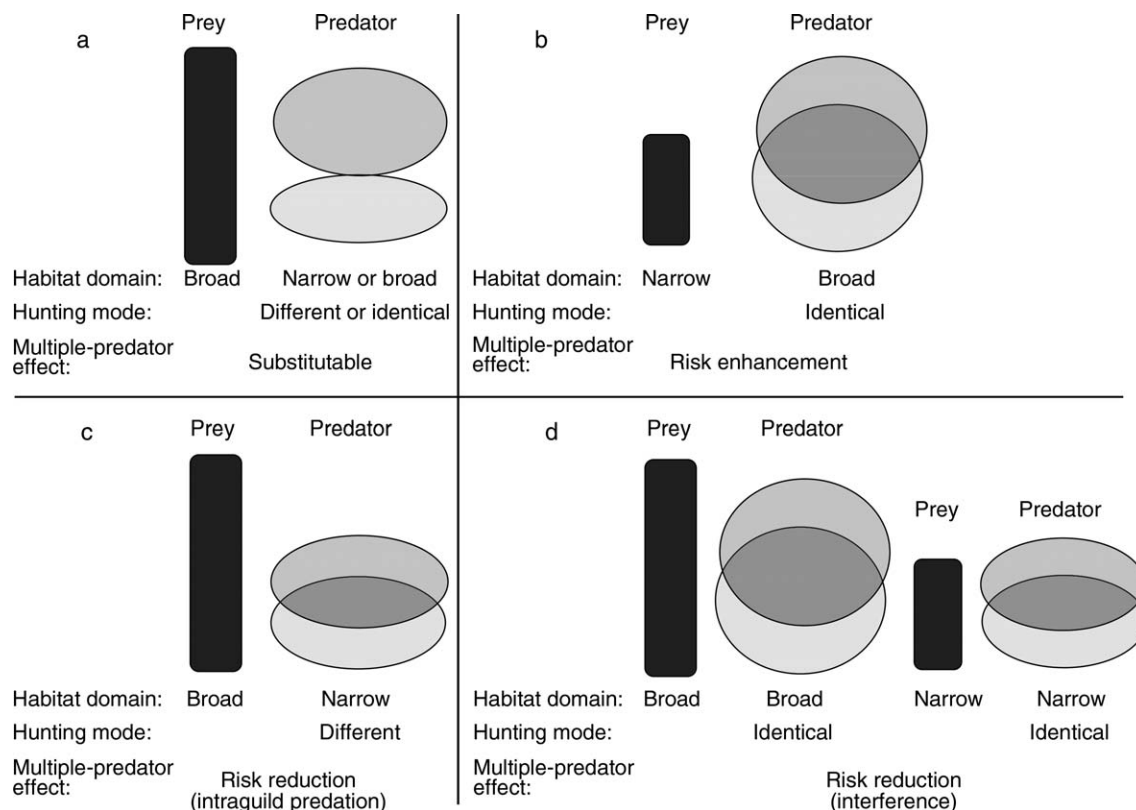


FIG. 2. Predictions of four contingent multiple-predator effects on a common prey species derived from an empirical synthesis of multiple-predator experiments. Dark rectangles represent the prey habitat domain. Ellipses represent predator habitat domain. (a) Predators are expected to have substitutable effects whenever prey have broad habitat domains and predators have complementary (narrow or broad) habitat domains. (b) Predators are expected to have risk-enhancing effects whenever prey have a narrow domain and predators have broad, overlapping habitat domains and the same hunting modes. (c) Predators are expected to have risk-reducing effects due to intraguild predation whenever prey have a broad domain and predators have narrow, overlapping habitat domains and different hunting modes. (d) Predators are expected to have risk-reducing effects due to interference interactions when they have identical hunting modes and overlapping habitat domains with themselves and their prey.

“mean-field” encounter process is a reasonable approximation of the predation risk that is encountered throughout its habitat domain.

The alternative contingency, where prey species have narrow habitat domains and predator species have complementary habitat domains, is trivial because one predator species never encounters the prey. Hence, this contingency reduces to a single predator–prey system.

**Risk enhancement.**—Risk enhancement should occur whenever prey species have narrow habitat domains and predator species have the same hunting mode and broad but overlapping habitat domains (Fig. 2b). Risk enhancement arises for two reasons. First, the prey species’ habitat domain is nested within that of its predators. As a result, prey have limited recourse to escape their predators. Second, because predator species can roam more broadly than their prey, they are not totally reliant on that prey. They can seek prey elsewhere to subsidize their needs, thereby decreasing the chance of negative interactions. These conditions create a multiplicative (*sensu* Soluk and Collins [1988]; see also Sih et al. [1998]) rise in predation risk.

**Risk reduction.**—Two mechanisms can lead to risk reduction: intraguild predation and interference interactions. Intraguild predation should arise whenever prey species have broad habitat domains and predators have overlapping narrow habitat domains with different hunting modes (Fig. 2c). In this case, prey can evade predators by seeking spatial locations that neither predator accesses. With no other prey, predators hunt each other, and the asymmetry in hunting mode sets up conditions that foster this asymmetrical predator–predator interaction. Interference interactions arise when predator species have identical hunting modes and when both prey and predator have either broad or narrow habitat domains but overlap completely in space (Fig. 2d). These conditions cause predators to vie for and defend hunting locations in space. This in turn detracts from time spent hunting, thereby reducing the prey species’ risk of mortality.

A final contingency, prey with a broad habitat domain and predators with overlapping, narrow domains and identical hunting modes, has not yet been reported in the literature.

The empirical synthesis combined with the classification scheme for multiple-predator effects embodies five important points. First, evidence for predator substitutability means that simple food chain models that treat all predator species as a single functional group can offer biologically reasonable insights. So, classical food chain models may not necessarily oversimplify biological reality. Second, the effect of a predator species on trophic interactions will not be constant. It depends upon that species' hunting mode and habitat domain relative to that of the other predator species with which it is associated, i.e., there is context dependency. Third, the nature of a predator species' effect is predictable once natural history detail about its hunting mode and habitat domain and that of all other predator species in a system is known. Fourth, context dependency does not lead to inordinate complexity: there are effectively only four general kinds of multiple-predator outcomes. Fifth, risk enhancement due solely to multiple-predator effects appears to be highly unusual given the field systems studied thus far (Appendix B). This raises the prospect that predator species diversity per se may be generally unlikely to enhance prey species population control. In most studies, multiple predators either were equally effective as single predators in controlling a common prey species, or less so.

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The above predictions should be tested by titrating single and multiple predator species, with specific hunting modes and habitat domains, against prey with different habitat domains. These titrations also argue for using substitutive designs to avoid confounding predator and prey characteristics with predator density, or using a diagnostic test for substitutability (e.g., Eq. 4) if using additive designs.

Producing reliable insights about natural predator function also requires careful consideration of potential artifacts due to venue choice and venue size. For example, under natural conditions two predator species should have linear, substitutable effects on prey when they have complementary habitat domains (say, one broad and one narrow), and when they face a common prey with a broad habitat domain (Fig. 2a). Suppose, however, that one opted to execute a laboratory experiment to understand the effects of these species. But laboratory experiments create artificial habitat. If the artificial habitat constrained the prey and predator species' habitat domain such that they became narrower and more overlapping than in the field, one could see nonlinear risk reduction (Fig. 2d). The laboratory experiment thus would lead to an incorrect baseline understanding of the functional roles of these predators in nature. Nevertheless, altering natural habitat structure via artificial means represents a useful way to evaluate how altered habitat should change the nature of the predator diversity effects on trophic interactions

(Siddon and Witman 2004, Warfe and Barmuta 2004, Denno et al. 2005). But this should only be done once the natural baseline has been established. Conducting habitat manipulations with a focus on changing habitat domain and hunting mode, e.g., alteration of predator–predator interactions by constraining habitat domain, may also lead to clearer mechanistic insight. Such insights may apply to ecological theory that predicts food web dynamics will become altered if predators are compressed spatially (Holt 2002, McCann et al. 2005).

The habitat domain–hunting mode concept presented above is entirely qualitative. Making it operational requires specifying measurement criteria that can be applied in an experimental setting. An approach developed by Schmitz and Suttle (2001) proposes measuring the vertical and horizontal spatial movement of marked prey and predator individuals during sampling periods that cover replicate daily activity cycles and then calculating 95% confidence ellipses for the spatial movement by each species. These ellipses are then mapped onto the spatial extent of the habitat (e.g., see Schmitz and Suttle 2001: Fig. 1). As a starting rule of thumb, if the confidence ellipse (viz., habitat domain) covers 50% or more of the spatial extent of the habitat, then it is a broad domain; if it is less than 50%, then it is a narrow domain.

I also introduced, for simplicity, discrete categories of predator hunting mode (i.e., sit-and-wait, sit-and-pursue, active). In reality, hunting mode may be more graded due to predator flexibility with changing environmental conditions (Cooper 2005, Scharf et al. 2006). Such flexibility means that we need to go beyond treating predator and prey species as agents with fixed movement strategies and consider interactions in a more dynamic context (Lima 2002). The idea of hunting mode and habitat domain offers one way to begin making the idea of a dynamic interplay operational.

Different prey species may respond differently to the same predator species, and the response is dependent upon the prey species' own impetus or capacity to avoid predators within its own habitat domain (Relyea 2003, Schmitz 2005). The most successful hunting strategy will then depend on the nature of prey movement. For example, sit-and-wait hunting tends to be most successful when slow-moving predators face rapidly moving prey; active hunting tends to be most successful in opposite conditions (Huey and Pianka 1981, Scharf et al. 2006). Thus, a shift in prey species activity, through behavioral (or other antipredator trait) responses of prey, or a shift in the prey species composition of a system, may cause predators to shift their hunting mode. For example, actively hunting predators that increasingly face actively moving prey species may shift toward a comparatively more sedentary, sit-and-pursue hunting mode. This change may in turn lead to an altered habitat domain and an alteration in the nature of the predator species' interactions with other predator species. Thus conclusions about predator diversity effects derived

from much current short-term experimentation may change in the long run, as predators and prey adapt to each others' strategies. Yet the outcome may still be predictable once we know the new habitat domain and hunting mode of the players in the system.

Likewise, prey species may respond differently to different predators. The nature of predator avoidance appears to be related to a predator's habitat domain and hunting mode (Schmitz 2005). Sit-and-wait and sit-and-pursue predator species occupy narrow domains. Widely roaming prey species typically decreased risk of predation in these circumstances by moving to other microhabitat locations (Schmitz 2005). Alternatively, such behavioral shifts were not observed when prey faced widely roaming, active predator species. The difference in prey behavior may represent different degrees of risk aversion, which may be related to the amount of information prey have about predator presence (Sih 1992, Luttbegg and Schmitz 2000, Bouskila 2001). Comparatively sedentary predators have a continuous presence within a fixed habitat location, and so they may provide a persistent point-source cue of high risk to prey. Alternatively, actively hunting predators provide diffused, moderate cues throughout the microhabitat. In this case, prey must weigh considerable energetic and associated survival costs (which can be up to 25% of the daily energy budget [Schmitz 2005]) of remaining continuously vigilant to such predators, especially when a direct threat may not be imminent, against the likelihood of being encountered and captured. Thus, prey facing active predators may become chronically less responsive to such predators (Lima and Bednekoff 1999, Bouskila 2001).

Experiments have also shown that the densities of prey relative to predators can influence multiple-predator effects independently of habitat (Evans 1991, Peckarsky 1991, Aukema et al. 2004, Vance-Chalcraft et al. 2005, Griffen 2006). In theory, density changes of prey should not alter individual predator species capture success (Scharf et al. 2006) owing to saturating functional responses. This appears to be the case empirically (Evans 1991, Peckarsky 1991, Aukema et al. 2004, Vance-Chalcraft et al. 2005, Griffen 2006). However, changing prey densities via predator evasion may affect predator hunting mode and habitat domain as described earlier and shown empirically (Peckarsky 1991, Griffen 2006). Thus the concept presented here may also help to reconcile how prey density influences predator diversity effects on prey mortality.

Finally, growing evidence shows that there is consistency between the nature of multiple-predator effects observed on a prey species and on the prey species' resources (Spiller and Schoener 1994, Schmitz and Sokol-Hessner 2002, Lang 2003, Siddon and Witman 2004, Bruno and O'Connor 2005, Byrnes et al. 2006). For example, predators that have substitutable effects on their prey have substitutable indirect effects on the prey's resources (Schmitz and Sokol-Hessner 2002,

Bruno and O'Connor 2005, Finke and Denno 2005, Byrnes et al. 2006); predators that have risk-reducing effects on their prey have reduced indirect effects on the prey's resources (Lang 2003, Siddon and Witman 2004, Finke and Denno 2005). This offers some promise that knowledge of predator hunting modes and habitat domains may be key to predicting how predator diversity effects cascade through ecosystems.

### Conclusions

Merely conducting ever more experiments that just evaluate multiple-predator effects will simply enlarge the list of case studies. To develop general theory, we need to approach experimentation with a priori predictions that will lead to a coherent, mechanistic understanding of the ways that predator diversity affects ecosystems (Sih et al. 1998). I argue here that knowledge of predator and prey habitat domain and predator hunting mode may offer testable, mechanistic predictions about the nature of predator diversity effects on trophic interactions. If this hypothesis is supported by explicit tests, then predator species function can be specified simply on the basis of fundamental natural history understanding of predator hunting behavior and space use within habitats. Such understanding would offer powerful insight for assigning predator species into functional units and thereby help to develop biologically realistic models of trophic interactions.

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#### APPENDIX A

Mathematical derivation of conditions for substitutability in replacement series and additive experiments (*Ecological Archives* E088-144-A1).

#### APPENDIX B

Information used to reevaluate the conclusion about multiple-predator effects on prey drawn in studies that employed additive experimental designs (*Ecological Archives* E088-144-A2).

#### APPENDIX C

Ecological conditions (predator species habitat domain and hunting mode, and prey habitat domain) in experimental studies of multiple-predator effects conducted under field conditions (*Ecological Archives* E088-144-A3).