vol. 162, no. 4 the american naturalist october 2003

Mapping Functional Similarity of Predators on the Basis of Trait Similarities

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Submitted December 2, 2002; Accepted April 3, 2003;
Electronically published September 8, 2003

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abstract: Theoretical and empirical studies in community ecology often simplify their study system by lumping together species on the basis of trait similarities (e.g., their taxonomy, resource or microhabitat usage) and then assume species sharing similar traits are functionally similar. To date, no study has directly tested whether species more similar with respect to any of these traits are more similar in their functional effects on population or ecosystem processes. In this study, we examined the association between traits and functional effects of six different aquatic predatory vertebrates. We demonstrated that functional similarity across multiple response variables was not correlated with trait similarity, but differences in trait values were associated with significantly different effects on individual response variables. The exact relationship between species traits and functional effect of predators, however, was different for each response variable. Using traits to predict functional similarity among species may be useful when considering individual response variables, but only if it is known which traits have the greatest influence on the response variable of interest. It is doubtful that any one scheme will predict the functional similarity of species across a diverse array of response variables because each response will likely be strongly influenced by different traits.

Keywords: functional similarity, trait similarity, functional group, predation, trophic level.

A common practice in both theoretical and empirical ecology is to simplify food webs by lumping together species into a smaller number of groups designated as "kinds of organisms" (e.g., Cohen 1978; Briand 1983; Suigihara et al. 1989, 1997), guilds (e.g., Root 1967; Jaksić and Medel 1990; Wilson 1999), trophic levels (Hairston et al. 1960; Menge and Sutherland 1976, 1987; Fretwell 1977; Oksanen et al. 1981; McQueen et al. 1986; Ginzburg and Akçakaya 1992), or functional groups (e.g., Cummins 1974; Faber 1991; Walker 1991; Körner 1993; Hooper and Vitousek 1997, 1998; Smith et al. 1997; Chapin et al. 1998; Symstad et al. 2000). This practice assumes that all species within one group are more similar in their effect on population, community, or ecosystem processes (i.e., they are functionally similar) than they are to species within another group.[1] Although the identification of species is more reliably derived than the identification of functional groups (Gitay and Noble 1997; Naeem 2002), the lumping together of species in this manner has been advocated as the key to a number of issues in ecology and conservation (see review by Wilson 1999). A growing body of literature, however, suggests that different species may produce diverse effects on a community even though they occupy similar positions (e.g., predator) in the food web (Morin 1983; Paine 1992; McPeek 1998; Morin and Kurzava 1998; Schmitz and Suttle 2001; Chalcraft and Resetarits 2003). Thus, any scheme for identifying functionally similar species clearly must consider criteria beyond simple trophic position.

Within a trophic level, species are often considered to be more functionally similar if they are more similar with respect to certain easily identifiable traits, even though the connection between these specific traits and their functional effects are often unknown (Jaksić 1981; Hawkins and MacMahon 1989; Simberloff and Dayan 1991; Harris 1995; Lavorel et al. 1997; Dyer et al. 2001). For example, animal species that are more similar in terms of taxonomic relationships, food resources, or microhabitat use are often

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[1] Although the terms "functional effects" and "functional similarity" are most commonly used to describe the effect of plant and microbial species on ecosystem processes (e.g., primary productivity and nutrient cycling) through their usage of food resources, we extend usage of these terms to describe the effect of animal species on ecosystem processes (e.g., secondary productivity) and population processes (rates of population growth) through their use of food resources.

assumed to be more similar in functional effects than are animal species dissimilar with respect to such traits (e.g., Faber 1991; Walker 1991; Wardle et al. 1997; for reviews, also see Hawkins and MacMahon 1989; Simberloff and Dayan 1991).

Currently, it is unclear whether species more similar with respect to any of these traits (or a host of others used to classify functional groups) are more similar in functional effects than are species dissimilar with respect to these traits. This is essentially an unresolved empirical question made more important by the frequent practice in several active areas of ecological research of lumping together species on the basis of trait similarities. For example, species are often lumped into functional groups on the basis of traits in order to examine the consequences of biodiversity loss to ecosystem functioning (e.g., Aguiar et al. 1996; Hooper and Vitousek 1997, 1998; Symstad 2000; Symstad et al. 2000; Reich et al. 2001) and to examine patterns of species co-occurrence among different localities (e.g., Vuilleumier and Simberloff 1980; Graves and Gotelli 1993). Sih et al. (1998) have also suggested the use of species traits to predict the likelihood and direction of nonadditive effects on prey species in multiple predator studies.

Establishing a general relationship between species traits and species functional effects has been difficult to this point, however, because most studies have compared only two species within a trophic level (e.g., Morin 1983, 1995; Van Buskirk 1988; Fauth and Resetarits 1991; Kurzava and Morin 1998; Snyder and Wise 2001; Spiller and Schoener 2001). Although such pairwise studies demonstrate that species occupying similar trophic positions can have dissimilar effects, it is not possible to identify which traits or suite of traits are causing species to differ in their effects when only two species are considered. Furthermore, comparisons of different species possessing different traits across different studies are inappropriate because there is often substantial variation in the experimental protocols employed (e.g., variation in prey species, abundances, diversities, and environmental conditions). Although a number of studies have examined the relationship between environment and species traits (i.e., the response of a species to the environment; e.g., Reznick and Endler 1982; Dyer et al. 2001; Relyea 2001), Harris's (1995) work currently represents the only study to experimentally evaluate the relationship between similarity in traits and similarity in function of animals (i.e., the effect of a species).

To examine the relationship between trait similarity and functional similarity, Harris (1995) measured the effects of six pond species (two snails, two larval anurans, one fish, and one salamander) on other organisms (algae and microinvertebrates) in pond food webs. She concluded that, in her study, the pattern of functional similarity among the six pond species was effectively predicted by the pattern of trait similarity among species. This conclusion was based on the fact that four species representing two different phylogenetic lines (snails and larval anurans) were classified in one group as herbivores, while the fish and salamanders represented two different groups of predators. Although herbivores obviously consumed different resources than the predators, it was not possible to divine any criteria to indicate why the two predators differed. Furthermore, Harris (1995) and Wilbur (1997) urged caution in treating the herbivores as functionally equivalent because the experimental protocol most likely did not allow detection of differences early in the experiment when all species were present. As a result, we believe that it is obviously possible to use species traits to distinguish among trophic levels (e.g., separate predators from herbivores), but it is unclear what traits are useful for describing the differential effects of species within a trophic level.

We previously demonstrated that different species occupying the predator trophic position in pond food webs have significantly different effects on an assemblage of grazing larval anurans (Chalcraft and Resetarits 2003). Here, we focus on establishing a conceptual framework and specifically examine whether predators more similar in terms of taxonomy, food resources, or usage of microhabitats are more similar in their functional effects than predators dissimilar with respect to these traits. Furthermore, we evaluate the relative degree to which each trait accounts for variation in the functional effects of predators in order to determine which traits are associated with greater differences in these functional effects. The information we document here is essential for enabling us to better understand the consequences of biodiversity loss, since it would enable us to quantify functional diversity in a particular ecosystem (Walker et al. 1999; Petchey and Gaston 2002*a*, 2002*b*).

It is important to note that throughout this article, we do not assume predators sharing a similar trait value are equivalent in effect. Rather, we examine whether the average effect of predators possessing a particular trait differs from the average effect of predators possessing a different trait. Because it has been suggested that functional similarity among predator species may be dependent on the degree of resolution of the response variable (Kurzava and Morin 1998), we evaluated the relationship between species traits and species functional effects with response variables representing both a coarse aggregate measure across all prey species (e.g., the total biomass or total number of all prey) and a species-specific prey response (e.g., the survivorship of each individual prey species). Clearly, the degree to which species traits can be successfully mapped on functional effects determines the overall utility of lumping species together.

Study System

Six different aquatic vertebrate predators are commonly found in ponds at our study site on the eastern edge of the Great Dismal Swamp (Naval Security Group Activity Northwest [NSGANW]) in southeastern Virginia. From a taxonomic standpoint, these predators can be easily divided into two distinct groups: fish (*Enneacanthus obesus*: Centrarchidae; *Gambusia holbrooki*: Poeciliidae; and *Umbra pygmaea*: Umbridae) and salamanders (*Ambystoma opacum*: Ambystomatidae; *Amphiuma means*: Amphiumidae; and *Notophthalmus viridescens*: Salamandridae). This particular grouping of predators is common in aquatic studies, and differences in the functional roles represented by predatory fish versus salamanders are thought to have a dramatic effect on pond communities (Heyer et al. 1975; Bronmark and Edenhamn 1994; Werner and McPeek 1994; Wellborn et al. 1996; Hecnar and M'Closkey 1997; Skelly 1997; McPeek 1998). We hypothesized that the average effect of fish on their amphibian prey would be significantly stronger than that of salamanders because aquatic ecologists suggest that intensity of predation in ponds with fish is greater than in fishless ponds. Furthermore, in this specific case, we also hypothesized that taxonomic differences among predators would account for more variation in effect than other species traits because ecologists frequently separate aquatic habitats on the basis of whether fish or other predators dominate. Any differences in the effects of fish and salamanders can be the result of differences in a variety of specific traits (e.g., swimming speed, visual acuity, etc.) that are associated with taxonomic affiliation.

In addition to differences in taxonomic relationships, these predators also differ in use of microhabitats and relative gape sizes. Although most occur in the water column (i.e., they are pelagic), *Amphiuma* and *Umbra* generally occur in or along the bottom (i.e., they are benthic; Bishop 1947; Murdy et al. 1997; Petranka 1998; D. R. Chalcraft, personal observation). These predators can easily be ranked by their gape size on the basis of a visual comparison of predator mouth morphology: *Amphiuma* and *Enneacanthus* have the largest gape sizes, while *Notophthalmus* and *Gambusia* have the smallest; larval *Ambystoma* and *Umbra* are intermediate in gape (D. R. Chalcraft, personal observation). This ranking of gape size parallels the ranking of predator body sizes with the exception of *Notophthalmus* and *Ambystoma* (Bishop 1947; Murdy et al. 1997; Petranka 1998). Both *Notophthalmus* and larval *Ambystoma* are similar in body size, but *Ambystoma* have a much wider head than *Notophthalmus* (Bishop 1947; Petranka 1998; D. R. Chalcraft, personal observation). Gape size is an especially important factor to consider in predator-prey interactions, particularly in aquatic systems, because the size of the mouth can limit the size range of food resources available to the predator (Ebenman and Persson 1988; Persson et al. 1996).

We hypothesize that if microhabitat use is correlated with a predator's functional role, pelagic and benthic predators will differ in their effect on pond communities. Furthermore, we hypothesize that the effect of predators will increase with gape size. It is important to note that, as in practice, all species identified in a particular trait (functional) group may not be equivalent in the degree to which they express that trait. Species within a particular trait group, however, are more similar in the extent to which they display a particular trait. For example, *Amphiuma* and *Umbra* may differ in the extent to which they are benthic, but both are clearly more benthic than the other predators. This is similar to the manner in which ecologists use their understanding of species natural history to assign animals into guilds or functional groups (Jaksić 1981; Hawkins and MacMahon 1989; Simberloff and Dayan 1991).

In this study, we focused on the impact of each of these predators on three of the four larval anuran species that bred in ponds at NSGANW during the spring of 2000. These anurans were *Pseudacris crucifer*, *Rana sphenocephala*, and *Bufo terrestris*. All three use a broad array of breeding sites. *Pseudacris* and *Bufo* have relatively short larval periods of 1 to several months and metamorphose at relatively small sizes. *Rana* typically has a longer larval period and metamorphoses at a relatively large size. After hatching, each species is initially susceptible to predation by all of the predators in this study, but as they grow, they can escape from predators with smaller gape. All three species are grazers of periphyton and phytoplankton; *Rana* and *Bufo* are similar in competitive ability, while *Pseudacris* is competitively inferior to both (Morin 1983; Kurzava and Morin 1998; Chalcraft 2002). Competitive ability in larval anurans is tightly correlated with activity levels and often involves trade-offs with susceptibility to particular predators. Furthermore, the susceptibility of larval anurans to predation may be dependent on predator microhabitat, since some larval anurans become more benthic in the presence of predators (e.g., Morin 1986; Lawler 1989).

Methods

We conducted the experiment in 28 1,000-L cattle tanks designed to mimic natural ponds (Morin 1983). This experiment contained seven treatments: six corresponding to the identities of the six different predators and the seventh (control) representing the absence of predators. Each treatment was replicated four times within a randomized complete block design.

Before the application of any of the following methods, we identified four spatial clusters of seven ponds each to represent statistical blocks. Ponds within a block are closer together and should respond to any unknown spatial gradients in a similar manner. Furthermore, we conducted any procedures (e.g., creation and monitoring of ponds) on all ponds within a block before performing them on any ponds in another block in order to minimize the amount of variation within blocks not attributable to treatments.

Tanks were filled from a nearby pond and received 1 kg of leaf litter on April 13–14, 2000. Pond water was filtered through 2-mm mesh, allowing zooplankton, phytoplankton, periphyton, and small invertebrates to pass but excluding larger invertebrates and vertebrates. After filling, each tank was covered with a tight-fitting screen lid to prevent unwanted colonization and to contain experimental animals. On April 15, 2000, we added a 500-mL mixture of zooplankton, periphyton, and phytoplankton collected from a variety of ponds and ditches at NSGANW to supplement the existing complexity. On April 24, 2000, we added 175 (each) newly hatched *Pseudacris*, *Rana*, and *Bufo* tadpoles to each tank. One day after adding the prey species, we randomly assigned one of the seven treatments to each of the seven ponds within a block. Predator treatments received two individuals of the designated species with the exception of ponds designated to contain *Amphiuma*, which received one individual. The lower density reflects the fact that *Amphiuma* is larger and naturally less abundant. Predators within each species were ranked by size, and each block received predators of the same rank size to ensure that comparisons among species within a block represented comparisons of similar regions of the size distribution for each species. Thus, any effects associated with intraspecific variation in predator body size are confounded with differences among blocks. Initial densities of all larval anuran and predator species fell within the range observed in natural ponds (Morin 1983, 1995; Bristow 1991; D. R. Chalcraft, personal observation).

We monitored ponds on a daily basis and collected anurans as they metamorphosed (defined as emergence of at least one forelimb). Metamorphs were weighed on tail resorption. Date of collection and wet mass (g) were recorded for each individual. Between June 22 and 25, 2000, we drained all ponds and thoroughly searched the leaf litter to produce a complete census of surviving anurans and predators. Remaining animals were brought back to the lab, and wet mass (g) of each individual was recorded.

We measured the effect of each predator species on five response variables: total biomass of all surviving anurans (metamorphs and tadpoles), total number of all surviving anurans (metamorphs and tadpoles), and survivorship of each prey species. The first two response variables represent alternative measures of the importance of the larval anuran assemblage to the pond food web (more larval anurans indicate that more algae will be consumed), while the last three represent a measure of performance for each prey species. Both measures of importance were examined because the degree of similarity in the effects of predators on each measure are different (Chalcraft and Resetarits 2003). Per capita effect of each predator species on each response variable was measured relative to control tanks according to the following formula:

$$\frac{\ln (E/C)}{N}, \tag{1}$$

where E is the value of the response variable in a tank with a particular predator, C is the value of the response variable in a tank with no predators, and N is the number of predators in that tank (Laska and Wootton 1998); E and C values were derived from tanks within the same spatial block. Positive values indicate that predators enhance the value of the response variable relative to the control, while negative values indicate that predators reduce the value of the response variable relative to the control. Hereafter, we use the terms "effect" and "per capita effect" synonymously.

We determined whether similarity across all of the predator traits considered was associated with the level of functional similarity across multiple response variables using a Mantel test of association. The Mantel test is useful because it is a nonparametric test that determines whether there is an overall correlation between similar cells in two matrices while accounting for lack of independence among similarity values within a matrix (Manly 1994). To do this, we first constructed three matrices that described the degree of similarity among each predator species in terms of their taxonomies, microhabitat usage, and gape size, their functional effect on both aggregate response variables, and their functional effect on each individual prey species simultaneously. The degree of functional similarity between species pairs was determined using the mean effect vector (e.g., the vector describing the per capita effect of a predator species on the survivorship of each prey species) of the six predators. We chose the mean effect vector because Harris (1995) argued that it provided a better relationship between trait similarity and functional similarity than using the effect of predators in each individual replicate. To calculate similarity between predators using the categorical trait descriptions used in this study (e.g., fish or salamander), we numerically coded trait values for each trait independently. Our measure of similarity between predator species was the euclidean distance between their mean effect or trait vectors (Manly 1994). The significance of a correlation between the trait similarity matrix and each of the two effect matrices was determined by comparing the observed Mantel test statistic (Z) to a distribution of Z statistics that was derived from 720 iterations of randomly altering the location of cell values in one matrix (Manly 1994). There are 720 possible ways to randomly arrange cell values in a 6×6 matrix. Two matrices are considered to be significantly correlated if the observed Z value is greater than 95% of the Z values calculated from the random iterations. The Mantel tests were performed using Passage software (Rosenberg 2002).

To evaluate whether differences in the effects of different predators on each response variable is the result of differences in specific traits, we used planned orthogonal contrasts embedded within ANOVA (table 1). The first contrast evaluated whether differences in the taxonomic relationships of predators produced significant differences in predator effects by comparing fish versus salamanders. It is important to note that each species represents an independent estimate of the effect for their respective taxonomic group, since each group is represented by three different families. The second and third contrasts evaluated whether differences in predator gape size produced significant differences in predator effects by comparing predators possessing either a small, intermediate, or large gape. The fourth contrast evaluated whether differences in a predator's use of microhabitats produced significant differences in effect by comparing benthic versus pelagic predators. Although *Gambusia* and *Notophthalmus* are both pelagic predators, their effects were not included in the microhabitat contrast in order to maintain orthogonality. Furthermore, none of our benthic predators has a gape similar in size to *Gambusia* and *Notophthalmus*.

It is not possible to evaluate the interactive effects of different traits because many of the possible trait combinations required for this analysis are not represented by any predator found in our study area. We did not include predator body size as a covariate because a supplemental analysis indicated that differences among treatments (for any response variable) within a block did not result from differences in ln(body size) (all F ratio's > 0.65, all P values $> .429$, all df $= 1, 19$).

The orthogonal nature of these contrasts is an important component of this study. Since sums of squares (SS) are additive for orthogonal contrasts (Sokal and Rohlf 1981), the SS associated with each contrast j (SS_j) provides an independent estimate of the total variation in predator effects attributable to differences in a particular trait. The relative degree to which each trait accounts for variation in the functional effects of predators is therefore calculated by

$$\frac{\mathrm{SS}_j}{\mathrm{SS}_{\mathrm{total}}} \times 100, \qquad (2)$$

where $\mathrm{SS}_{\mathrm{total}}$ provides a measure of the total amount of variation in predator effects documented in the study. This is similar to the procedures reported by others (e.g., Wilbur 1983; Morin 1984; Welden and Slauson 1986) who evaluate the relative importance of independent factors in a factorial ANOVA.

Results

The degree of trait similarity among predator species was not significantly correlated with predator functional similarity across multiple response variables regardless of whether only aggregate ($r = 0.16$, $Z = 26.77$, $P = .266$) or species-specific response variables ($r = -0.08$, $Z = 35.16$, $P = .414$) were considered. As we illustrate later, however, trait similarity was correlated with functional similarity when only one response variable is considered at a time. Differences in the effects of predators on total anuran biomass were primarily the result of differences between predators with small gape versus intermediate or large gape (table 2). Predators with small gape had a negligible impact on total herbivore biomass, while predators with intermediate or large gape caused significant reduc-

Table 1: Planned contrasts used to compare functional group classification schemes

Contrast	*Amphiuma*	*Ambystoma*	*Enneacanthus*	*Gambusia*	*Notophthalmus*	*Umbra*
1. Taxonomy	+1	+1	−1	−1	+1	−1
2. Gape: S vs. M + L	+1	+1	+1	−2	−2	+1
3. Gape: M vs. L	+1	−1	+1	0	0	−1
4. Microhabitat	+1	−1	−1	0	0	+1

Note: Contrast 1 compares the effects of amphibian (+) and fish predators (−). Contrasts 2 and 3 compare the effect of representative predators that have a lower (+) or higher (−) degree of gape limitation that limits the range of consumable food items; L indicates predators with the largest gape, M indicates predators with an intermediate gape, and S indicates predators with the smallest gape. Contrast 4 compares the effect of representative pelagic (+) and benthic foraging (−) species. A zero in any given contrast indicates that the results for that particular species were not used in that particular contrast. All contrasts are orthogonal to one another; hence, their hypothesis sums of squares are additive.

Table 2: Planned orthogonal contrasts comparing the effects of predators on total herbivore biomass, total herbivore number, and the survivorship of *Bufo*, *Rana*, and *Pseudacris*

Source	SS	Importance (%)	df	*F*	*P*
Total herbivore biomass:					
Block	.553		3	3.96	
Contrasts:					
Taxonomy	.984	25.4	1	21.15	<.001
Gape		36.4			
S vs. M + L	1.376	35.5	1	29.59	<.001
M vs. L	.036	.9	1	.77	.395
Microhabitat	.005	.1	1	.10	.751
Error	.698		15		
Total	3.875				
Total herbivore number:					
Block	.043		3	.33	.800
Contrasts:					
Taxonomy	.700	4.4	1	16.04	.001
Gape		24.1			
S vs. M + L	1.982	12.4	1	45.44	<.001
M vs. L	1.868	11.7	1	42.81	<.001
Microhabitat	7.238	45.4	1	165.90	<.001
Error	.654		15		
Total	3.875				
Survivorship of *Bufo*:					
Block	.445		3	1.49	.257
Contrasts:					
Taxonomy	3.013	9.2	1	30.30	<.001
Gape		1.0			
S vs. M + L	.287	.9	1	2.89	.110
M vs. L	.027	.1	1	.27	.609
Microhabitat	21.528	65.4	1	216.50	<.001
Error	1.492		15		
Total	32.893				
Survivorship of *Rana*:					
Block	.276		3	1.13	.368
Contrasts:					
Taxonomy	2.206	14.6	1	27.13	.001
Gape		43.3			
S vs. M + L	5.631	37.4	1	69.24	<.001
M vs. L	.882	5.9	1	10.84	.005
Microhabitat	.029	.2	1	.36	.558
Error	1.220		15		
Total	15.068				
Survivorship of *Pseudacris*:					
Block	9.435		3	26.17	<.001
Contrasts:					
Taxonomy	13.714	47.9	1	114.10	<.001
Gape		2.8			
S vs. M + L	.636	2.2	1	5.29	.036
M vs. L	.176	.6	1	1.46	.245
Microhabitat	.351	1.2	1	2.92	.108
Error	1.803		15		
Total	28.632				

Note: The taxonomy contrast compares the effects of predatory fish and salamanders. The two gape contrasts compare the effects of predators having a relatively large (L), intermediate (M), or small (S) gape to differentiate predators that have a wider versus a narrower range of potential food items. The microhabitat contrast compares the effect of benthic and pelagic predators. Importance refers to the relative percentage of the total sums of squares (SS) that is explained by differences in contrast (trait) effects.

tions in total anuran biomass (fig. 1*A*). Intermediate- and large-gaped predators did not differ in their effects on total anuran biomass (table 2). A significant amount of variation in predator effects (25.4%) was the result of differences in the taxonomic relationships of predators (table 2). Fish caused a greater reduction in total anuran biomass than did salamanders (fig. 1*A*). Predators differing in their use of microhabitats did not differ in their effect on total anuran biomass (fig. 1*A*; table 2).

Microhabitat use explained the greatest amount of variation in the effects of predators on total number of anurans (table 2). Pelagic predators had a much greater effect on number of anurans than did benthic predators (fig. 1*B*), while differences in gape size also explained a significant amount of variation (24.1%; table 2). The effect of predators on the total number of anurans increased as gape size increased (fig. 1*B*). Although predators differing in their taxonomic relationships differed in effects on the total number of anurans (fig. 1*B*; table 2), taxonomy accounted for only a small fraction of that total variation.

Variation in the impacts on survivorship of *Bufo* was primarily associated with variation in the usage of microhabitats by the predators (table 2). Pelagic predators had strong negative effects on the survivorship of *Bufo*, while benthic predators had a negligible effect (fig. 2*A*). Although salamanders had a significantly stronger negative impact on *Bufo* survivorship than did fish (fig. 2*A*), taxonomic differences among predators only explained a small proportion of the total variation in predator effects (table 2). Predators that differed in gape did not differ in their effect on the *Bufo* survivorship (fig. 2*A*; table 2).

Gape size explained the greatest amount of variation in the effects of predators on survivorship of *Rana* (table 2). This effect significantly increased as gape size changed from small to large to intermediate values (fig. 2*B*). Fish had a significantly greater negative effect on *Rana* than did salamanders (fig. 2*B*), but taxonomic differences only accounted for 14.6% of the variation in predator effects (table 2). Predators differing in microhabitat use did not differ in effects on *Rana* (fig. 2*B*; table 2).

Differences in predator taxon explained the greatest amount of variation in survivorship of *Pseudacris* (table 2); salamanders enhanced the survivorship of *Pseudacris*, while fish reduced the survivorship (fig. 2*C*). Although small-gaped predators enhanced *Pseudacris* survivorship relative to the effect of predators with larger gapes, differences in predator gape size accounted for a very small fraction of effects on survivorship (fig. 2*C*; table 2). Predators differing in microhabitat did not differ in their effects on survivorship of *Pseudacris* (fig. 2*C*; table 2).

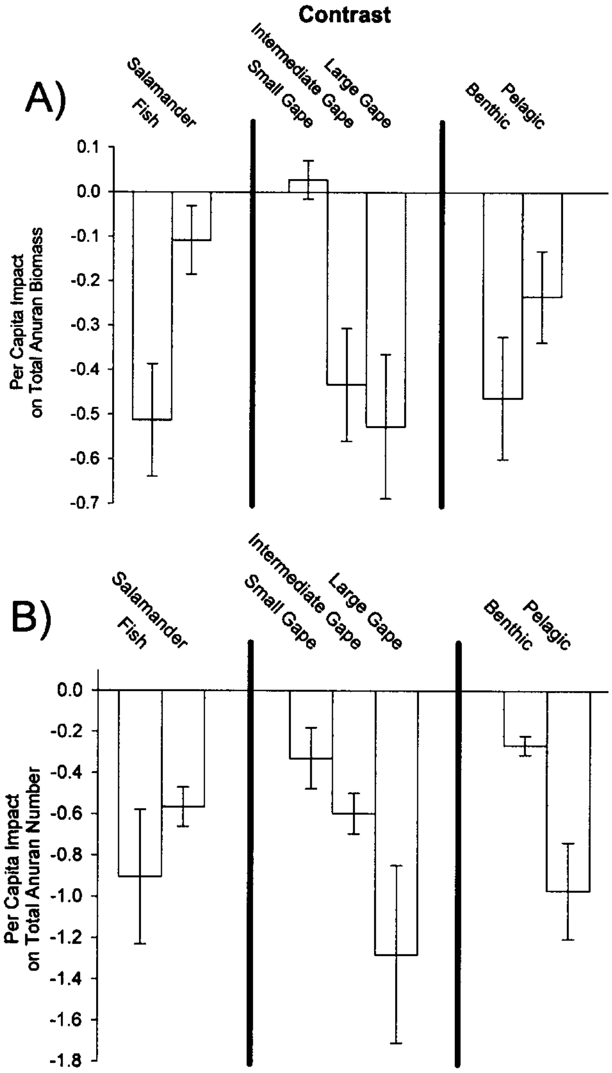

Figure 1: Mean (± 1 SE) per capita impact of seven different predator groupings on (*A*) total anuran biomass and (*B*) total anuran number. Solid vertical lines separate groups of predators associated with the three general contrasts (taxonomy, resource use, and microhabitat).

Discussion

Results of these analyses demonstrate that the functional effects of predators on prey responses are indeed related to differences in the values of traits commonly used to identify functional groups of animals. However, this only applies if individual response variables are treated one at a time; each of the five response variables we considered mapped differently on the three traits used to classify our predators into functional groups. Hence, functional similarity among predator species with respect to individual response variables is related to patterns of trait similarity, but there is no association between trait similarity and functional similarity when several response variables are considered (fig. 3*A*, 3*B*). Species sharing the same trait value will be more similar in effects to one another than to species having a dissimilar trait value, but only with respect to individual response variables. Thus, even though predators may be distributed along a continuous gradient ranging from weak effects to strong effects with respect to specific response variables (Chalcraft and Resetarits 2003), the position of each predator is largely dependent on taxonomy, gape size, and/or microhabitat use.

Relyea (2001) reached a conclusion similar to ours when he determined that the suite of antipredator defenses displayed by larval anuran prey is not correlated to the specific risk of predation imposed on them. His conclusion was surprising given that the degree to which some defense mechanisms are elicited is often correlated with predation risk (Sih 1987; Lima and Dill 1990; Short and Holomuzki 1992; Peckarsky 1996). To explain this difference, Relyea (2001) proposed that each prey species displays a characteristic suite of antipredator defenses to different predators irrespective of the specific level of predation risk. Why is there such specificity in the suite of antipredator responses to different predators? We believe specificity exists because each antipredator defense mechanism is most likely initiated by, and evolves to counter, different predator traits. Some defense mechanisms may relate to degree of predation risk, while others may result from the manner in which risk is imposed rather than the degree of risk. Furthermore, species may lack the ability to elicit certain morphological or behavioral responses even though similar species may exhibit them (McPeek 1990; McPeek et al. 1996). As a result, when responses are examined as a group, there is little association between the suite of defenses and specific predation risk.

Since all traits did not contribute equally to determining the likelihood that species will have similar effects on a particular response variable, a hierarchal approach to functional similarity may be best (Lavorel et al. 1997). This hierarchal approach applies if the order in which traits are applied to identify functionally dissimilar species is consistent with the relative importance of each trait for explaining the differences in effects (fig. 3*C*–3*E*). Because the sum of the independent effects associated with changes in each of these three traits explain a large proportion of the total variation in predator effects on a particular response variable (from 51.9% to 75.6%), the likelihood of predicting which species are more functionally similar on the basis of their traits (given the caveat of specifying response variables) appears to be relatively good. However, functionally similar in this context does not imply functional equivalence.

Furthermore, differences in the effects of predators associated with a particular trait were not always consistent with predictions. For example, fish had the greater impact on survivorship of *Rana*, but salamanders had the greater impact on survivorship of *Bufo*. Fish only had consistently stronger effects when the response variable considered represented an aggregate measure (i.e., total biomass or total number) across the prey species. Similarly, the relative effects of predators did not always increase with gape size even when gape explained a significant amount of variation in predator effects (e.g., fig. 1; fig. 2*B*, 2*C*). This indicates that although specific traits may be useful in detecting which species will be more (or less) similar, they do not allow us to predict reliably which predators will have stronger versus weaker effects on any given response variable.

In aquatic systems, taxonomy is a common way to differentiate the effects of different predators (Heyer et al. 1975; Bronmark and Edenhamn 1994; Werner and McPeek 1994; Wellborn et al. 1996; Hecnar and M'Closkey 1997; Skelly 1997; McPeek 1998). Our analyses demonstrate that predator taxonomy was the only trait to consistently differentiate among the effects of different predators across the different response variables. Taxonomy, however, often only accounted for a small percentage of the total variation in predator effects (e.g., table 2). In fact, difference in taxonomy was the most important trait differentiating among predators for only a single response variable (*Pseudacris* survival). This demonstrates that although fish and salamanders statistically differ in their effects, taxonomy may only be associated with subtle differences for certain response variables; in general, it has very little predictive power. In addition, even though salamanders may have weaker effects than fish on aggregate response variables, the difference is not always large (fig. 1).

Although the functional effects of predators on individual response variables are associated with specific traits of the predator, which allows us to map predator effects on predator traits, the traits that were most useful for differentiating among predators differed for each response variable (fig. 3*C*–3*E*). For example, microhabitat use best differentiated predator impacts on *Bufo*, gape was the best predictor of predator effects on *Rana*, and taxonomic relatedness best predicted effects on *Pseudacris*. This severely limits the utility of using functional groups as characterizations of functional roles in a general sense, but it strengthens the idea that predator effects on natural communities depend on relationships between specific characteristics of predator and prey. Different predator traits are most likely important for different prey species because prey differ in a number of traits that relate specifically to traits of the predators. Microhabitat use by predators is likely more important for *Bufo* than for other prey species because *Bufo* does not appear to restrict its foraging activities to the bottom in the presence of predators (D. R.

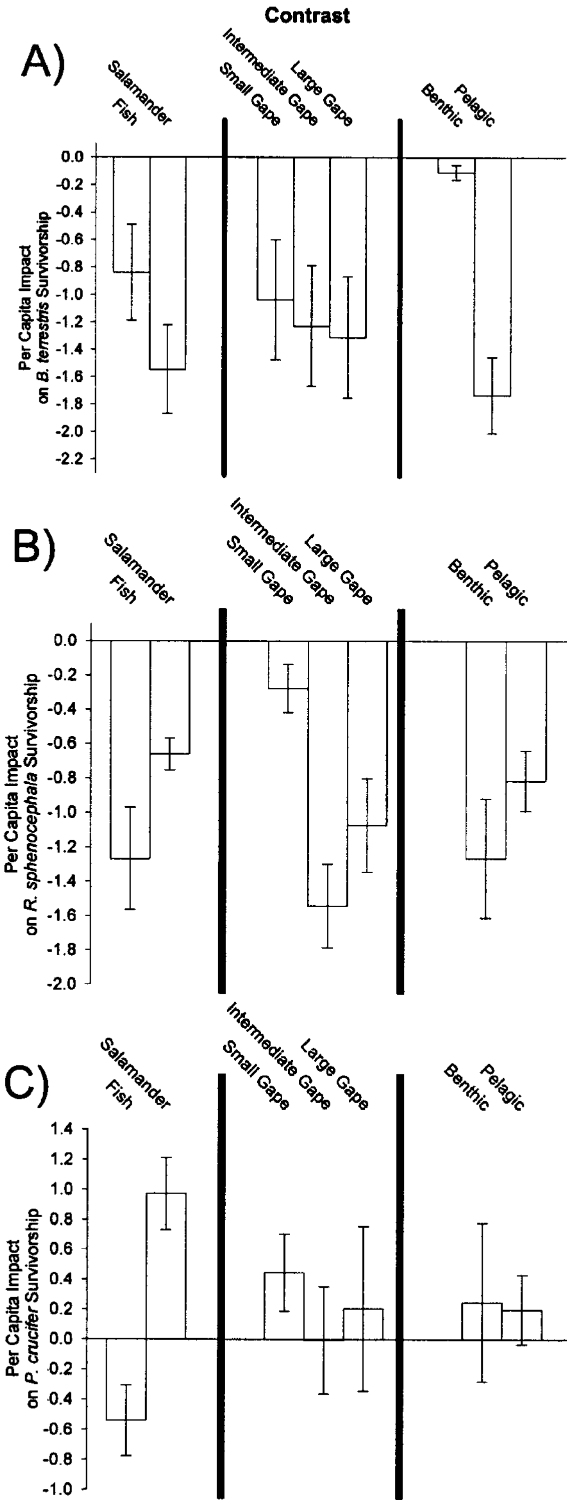

Figure 2: Mean (±1 SE) per capita impact of seven different predator groupings on the survivorship of (*A*) *Bufo*, (*B*) *Rana*, and (*C*) *Pseudacris*. Solid vertical lines separate groups of predators associated with the three general contrasts (taxonomy, resource use, and microhabitat).

Chalcraft, personal observation; note that Lawler [1989] observed a different species of *Bufo* foraging along the bottom of aquaria in the presence of predators). Although *Rana* and *Pseudacris* do preferentially forage on the bottom in the presence of predators, this strategy does not appear to be effective in reducing their risk of predation to predators that differ in their use of microhabitats. Gape size is more important for differentiating the effects of predators on *Rana* than for the other prey species because *Rana* grows to be the largest and can more easily escape from predators with smaller gapes. Taxonomy may be more important for *Pseudacris* than the other prey species because it tends to be less active than the other prey species (Morin 1983; Lawler 1989; D. R. Chalcraft, personal observation). Differences in the activity of anurans may cause visually oriented predators (such as fish and salamanders) to differ in their effects on *Pseudacris* if fish and salamanders differ in their visual acuity or actuation thresholds.

The result of this trait variability among both predator and prey species is that the utility of using individual traits or suites of traits to predict predator functional similarity will depend on the identity of the response variable considered. Thus, not only is it difficult to predict the extent of functional similarity among predators (Chalcraft and Resetarits 2003) but it is also difficult to predict which criteria are most effective for identifying functionally similar species in any general sense. Ecologists should therefore be cautious in identifying functional groups, since no one trait or combination of traits is likely to describe the complete functional effect of a species on a range of population or ecosystem processes. This point is also supported by the fact that similarity in predator traits was not associated with similarities in the effects of predators across multiple aggregate or species-specific response variables. This result indicates that the use of dendrograms for measuring functional diversity (as proposed by Walker et al. 1999; Petchey and Gaston 2002*a*, 2002*b*) may have limited applications, since multiple weighting schemes would have to be employed to describe the differential effects of species traits on multiple responses.

In summary, functional similarity maps on similarity in species traits but only one response variable at a time. Since the relationship between trait similarity and functional similarity is dependent on the specific response variable, it is unlikely that any one scheme of identifying functional similarity across multiple variables will be successful. Thus, the utility of the relationship between species traits and species functional effects is restricted to these individual response variables. This relationship is not trivial, however, in that it allows us to relate the range of adaptive responses in focal organisms—in this case, prey—to the range of predator traits to which they may be exposed. Identifying which traits are more important in de-

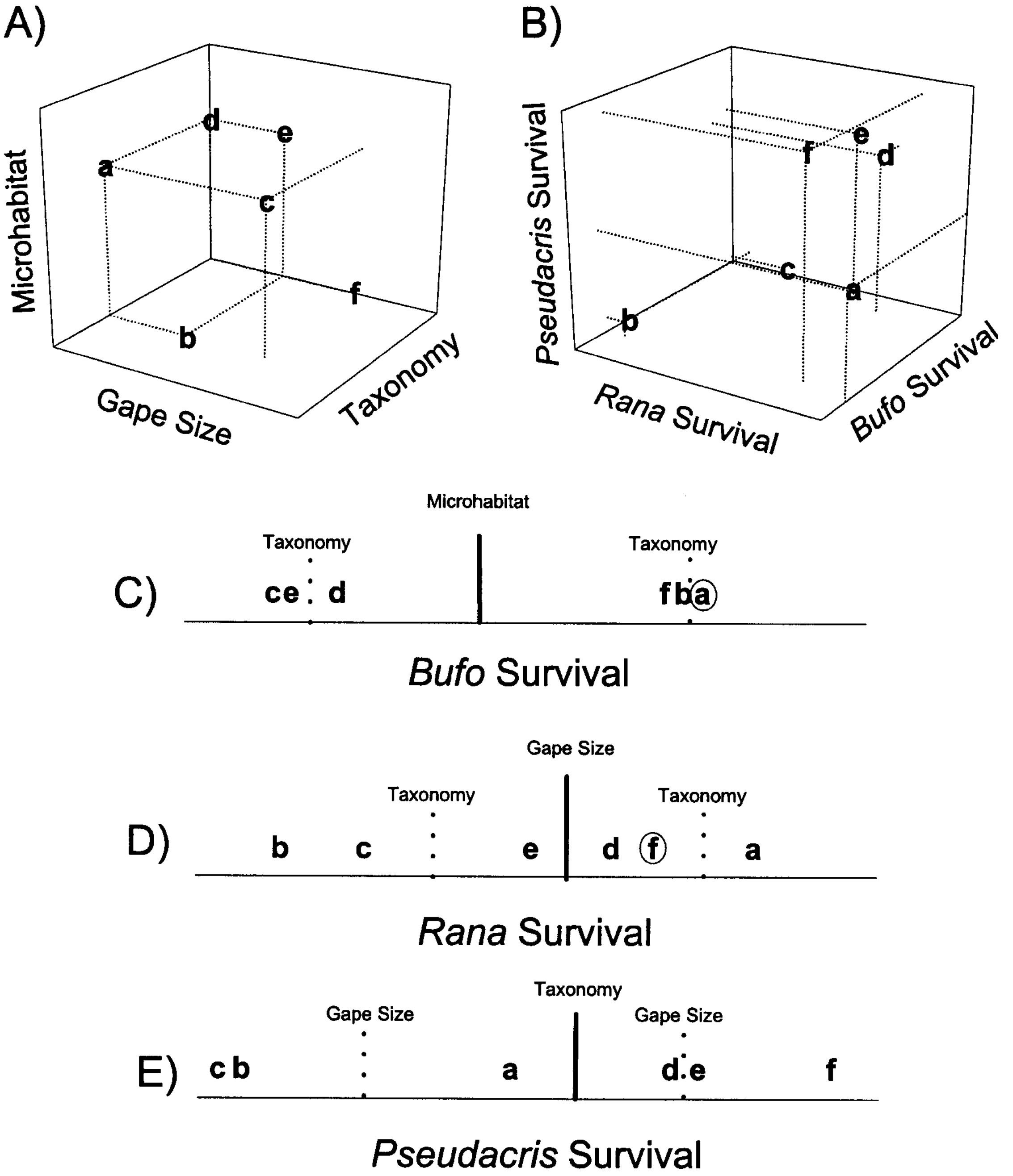

Figure 3: Conceptual illustration of the results of this study. The location of six different species (*a* = *Gambusia*, *b* = *Umbra*, *c* = *Enneacanthus*, *d* = *Notophthalmus*, *e* = *Ambystoma*, *f* = *Amphiuma*) in multidimensional space represented by (*A*) three different species traits and (*B*) three different functions. The locations of species in *A* and *B* do not correspond with each other; hence, there is no relationship between species traits and functional effects in multidimensional space. When each species is arranged in one-dimensional space for each function (*C*–*E*), the relative location of species can be predicted on the basis of trait similarities. In *C*–*E*, solid vertical lines separate species in functional space on the basis of differences in the value of the trait that has the greatest importance for determining a species function. Dotted vertical lines in *C*–*E* separate species in functional space on the basis of differences in the value of the trait that has the second greatest importance for determining a species function. Differences in gape size separate those predators having small mouths from those having a medium to large mouth, since the extent to which predators with medium and large gapes differed was often small. There are only two cases (indicated by circled letters) in which the location of a species along a function axis does not correspond with that predicted on the basis of species traits. Hence, a hierarchical approach of employing trait similarities can be useful in identifying which species will likely be more functionally similar. Note that the most important trait for determining a species function is different for each of the functions considered here; hence, the same trait map cannot be used for different functions.

termining functional similarity requires knowing how a given response variable is affected by those traits. As a result, similarity among species traits may provide an appropriate map (sensu Harris 1995) on which to predict similarities in the functional effects of species on individual response variables, but the same map will not be useful for other response variables (fig. 3*C*–3*E*). Thus, the assumption that species that look alike and act alike will have similar functional roles in a community is not supported in our study, because different prey species do not view predators in the same manner. Consequently, the identity of a functional group may more often be idiosyncratic rather than profoundly general. Ecologists should therefore be cautious in using species traits to lump species presumed to be ecologically similar, since the criteria by which functional groups are determined may have profound effects on the resulting conclusions (Gotelli and Graves 1996; Naeem 2002). It is possible, however, to identify species that are most similar in their ability to perform a specific function if care is taken to determine the relative importance of different traits in affecting a species' ability to perform a particular function. Lumping species into functional groups could be a valuable tool in ecological studies (see review in Wilson 1999) but only if the groupings truly reflect differences in the function of interest.

Acknowledgments

We would like to thank G. O. Batzli, C. Binckley, J. Brawn, C. Caceres, S. Kohler, K. Paige, J. Rieger, H. Vance-Chalcraft, and four anonymous reviewers for providing valuable comments on the manuscript. This project benefited from field assistance from C. Binckley, L. Gimson, N. Kyes, T. Maietta, J. Rieger, and J. True-Fowler and additional logistical support from the Center for Aquatic Ecology at the Illinois Natural History Survey and from R. Turner and the commanding officers, Naval Security Group Activity Northwest. Funding for this project was provided by a Sigma Xi grant, graduate student awards from the Illinois Natural History Survey and the Program in Ecology and Evolutionary Biology at the University of Illinois to D.R.C, a National Science Foundation (NSF) dissertation improvement grant (DEB-99-02188) to D.R.C. and W.J.R., and NSF (DEB-9727543) and Environmental Protection Agency–Science to Achieve Results (R825795-01-0) grants to W.J.R. The writing of a portion of this manuscript occurred while D.R.C. was supported as a postdoctoral associate at the National Center for Ecological Analysis and Synthesis, a center funded by the NSF (grant DEB-0072909) and the University of California, Santa Barbara.

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Associate Editor: Mathew A. Leibold