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PREDATOR IDENTITY AND ECOLOGICAL IMPACTS: FUNCTIONAL REDUNDANCY OR FUNCTIONAL DIVERSITY?

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Abstract. Different species occupy similar trophic positions in natural communities. However, ecologists have often overlooked the consequences of this variation for local communities by assuming that species occupying similar trophic positions are functionally similar. There have been few experimental tests of this important assumption. We tested the assumption of functional similarity by comparing the effect of six different predators (three fish and three salamander species) on an ensemble of larval anuran prey.

Our experiment identified substantial variation in the impact of different predators on a variety of responses. Differences among predators in their selection of prey caused the structure of the larval anuran ensemble to vary continuously as opposed to producing discrete alternative states. Predators also differed in their ability to suppress either the total number or biomass of anurans. Thus, performance of larval anurans was dependent upon the identity of the predator. Moreover, the identity of predators judged similar and their degree of similarity depends on the specific response variable. In our study we found no predominance of weak or strong interactors, as predators appear to be evenly distributed along a gradient of interaction strengths.

Knowledge of the identity of the species occupying a particular trophic position is crucial to predicting the impact of that trophic position on a community. Ecologists should not simply assume that species are functionally similar. The differing effects of different predators suggest that variation in their distribution across complex landscapes influences prey number, biomass, population dynamics, distribution, and ultimately local and regional species diversity.

Key words: beta diversity; community structure; fish; food web; keystone predation; larval anurans; ponds; predator–prey interactions; salamanders; species turnover; trophic level.

Introduction

Interactions among species influence individual fitness, population dynamics, and community structure (see reviews by Schoener 1983, Sih et al. 1985, Gurevitch et al. 1992, 2000, Bertness and Callaway 1994). An individual species, however, may co-occur with very different sets of species at different locations within its range. As a result, the occurrence and intensity of different types of species interactions (e.g., predation, competition, and mutualism) likely changes among locations. MacArthur and Wilson (1967) and Whittaker (1972) recognized this temporal and spatial change in species composition of local communities, calling it ‘‘species turnover’’ and ‘‘beta diversity,’’ respectively. Inherent in these ideas and much of what we call broadly ‘‘niche theory’’ is the notion that as species composition changes, so too does the precise nature of the species interactions.

An increasingly common practice in ecology, however, is to group species into ‘‘kinds of organisms’’ (e.g., Cohen 1978, Briand 1983, Sugihara et al. 1989, 1997), functional groups (e.g., Faber 1991, Walker 1991, Körner 1993, Hooper and Vitousek 1997, 1998, Smith et al. 1997, Chapin et al. 1998, Symstad et al. 2000), or trophic levels (e.g., Hairston et al. 1960, Menge and Sutherland 1976, 1987, Fretwell 1977, Oksanen et al. 1981, McQueen et al. 1986, Ginzberg and Akçakaya 1992). This approach assumes that all species so grouped act or respond similarly. Lacking this assumption, the grouping of species is meaningless in a predictive sense, and only serves to satisfy our need to simplify and categorize. The practice of grouping may contribute to the fact that the consequences of spatial and temporal variation in the species composition of local communities remain poorly understood.

Many authors have challenged this practice of grouping species for some time (e.g., Glasser 1983, May 1983, Cousins 1987, Paine 1988, Sugihara et al. 1989, Polis 1991, Polis and Strong 1996). Failure to consider turnover in species composition within trophic levels might produce the conflicting results that support opposing models of trophic structure (i.e., bottom-up vs. top-down effects; see Leibold 1989, 1996, Hunter and Price 1992, Leibold et al. 1997). Furthermore, much

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of the current debate concerning the relationship between biodiversity and ecosystem functioning focuses on the consequences of lumping species into functional groups (e.g., Aarssen 1997, Huston 1997, Allison 1999). Recently, some authors (Walker et al. 1999, Petchey and Gaston 2002*a*, *b*) have recognized the limitations of lumping species to derive estimates of functional diversity and have proposed alternative ways of measuring functional diversity.

Although grouping species has aided in the development of theory, the overall validity of the approach is essentially an empirical question: How similar are species within a trophic level in their effect on population, community, and ecosystem processes? Experiments designed to measure and compare the nature and strength of species interactions across a diverse array of species are necessary to (1) evaluate the assumption of functional similarity among species (Harris 1995, Morin 1995, Power et al. 1996, Kurzava and Morin 1998, Sih et al. 1998); (2) identify mechanisms responsible for theoretical and observed relationships between biodiversity and ecosystem function (Aarssen 1997, Huston 1997, Allison 1999); and (3) provide explanations for context-dependent support of theoretical models (Leibold 1989, 1996, Hunter and Price 1992, Leibold et al. 1997). Only a few studies, however, have simultaneously examined the strength of interactions among more than two species (e.g., Paine 1992, Rafaelli and Hall 1992, 1996, Goldwasser and Roughgarden 1993, Fagan and Hurd 1994, de Ruiter et al. 1995, Wootton 1997, Gomez and Zamora 1999).

In this study, we explore the consequences of variation in the identity of predators among local communities. Numerous studies have demonstrated that predators can have important effects in a diverse array of communities (Sih et al. 1985, Brett and Goldman 1997, Resetarits and Fauth 1998, Polis 1999, Chase 2000, Gurevitch et al. 2000). Studies have experimentally compared the effect of three (e.g., McPeek 1998, Schmitz and Suttle 2001) or more commonly two (e.g., Morin 1983, 1995, Van Buskirk 1988, Fauth and Resetarits 1991, Resetarits 1991, Harris 1995, Kurzava and Morin 1998, Snyder and Wise 2001, Spiller and Schoener 2001) predators; some show similarity of effects while others show marked differences. Few studies have compared a greater range of predators (e.g., McPeek 1990, Paine 1992, Rafaelli and Hall 1992, 1996, Goldwasser and Roughgarden 1993, de Ruiter et al. 1995, Relyea 2001), and only one (Paine 1992) has done so simultaneously under similar experimental conditions. Others compiled data from various experiments while McPeek (1990) and Relyea (2001) used short-term ($\leq$24 h) lab experiments. Thus, the extent of similarity across a greater range of species is unclear.

Here we report an experiment evaluating the consequences of variation in the identity of predators (six different species) for a common set of prey. Because the assessment of functional similarity among species within a trophic level may depend upon the scale of resolution (i.e., aggregate measures vs. species-specific measures) of the response variable (Kurzava and Morin 1998), we compare the effect of predators on several response variables that vary from ecosystem and community level parameters to individual species performance.

Study system

Ponds are ideal systems to examine the consequences of variation in predator identity among communities. First, the distinct water–land boundary defines an unambiguous border for each local community. Second, the identity of predators varies among ponds within small geographic regions and can change temporally within a given pond. Important components of pond communities that have served as a model system are algal grazing larval anurans. Numerous studies have demonstrated that predation plays an important role in their larval ecology (reviews: Wilbur 1997, Alford 1999).

Artificial ponds or mesocosms represent an important tool in experimental ecology (Wilbur 1987, Morin 1989, 1998, Fraser and Keddy 1997, Resetarits and Fauth 1998). Although scale is an important issue to consider in experiments that employ mesocosms (Pearman 1993, 1995, Petersen and Hastings 2001), previous experiments and field studies in natural ponds suggest that many processes identified as important in artificial ponds function similarly in their natural counterparts (e.g., Petranka 1989, Scott 1990, Semlitsch et al. 1996, Resetarits and Fauth 1998). Artificial ponds have been particularly useful for examining various aspects of amphibian larval ecology as a model system (see Wilbur 1997 for review).

In this study we focused on the effect of local variation in predator identity on an ensemble (sensu Fauth et al. 1996) of larval anurans consisting of *Bufo terrestris* (southern toad), *Rana sphenocephala* (southern leopard frog; see Plate 1), and *Pseudacris crucifer* (spring peeper). This represents all but one (*Pseudacris brimleyi* [Brimley's chorus frog]) of the late spring breeding anurans at our field site (Naval Security Group Activity Northwest [NSGANW]) located on the eastern edge of the Great Dismal Swamp in southeastern Virginia. Competition among these three species is often intense and asymmetric with *Bufo* and *Rana* being stronger competitors than *Pseudacris* (Morin 1981, 1983, Wilbur et al. 1983, Wilbur 1987, Fauth and Resetarits 1991, Chalcraft 2002). In a survey of potential local breeding habitats for anurans (i.e., ponds and ditches) at NSGANW during March and April 2000, we found eight predatory aquatic vertebrates. We evaluated the effect of the three most common fish (*Enneacanthus obesus* [banded sunfish], *Gambusia holbrooki* [mosquito fish], and *Umbra pygmaea* [eastern mud minnow]), and the three most common salamanders (larval *Ambystoma opacum* [marbled salamander],

PLATE 1. Tadpoles of the Southern leopard frog (*Rana sphenocephala*) represented one of the prey species used in an experiment designed to compare the functional effects of aquatic predatory vertebrates. Photo by D. R. Chalcraft.

Amphiuma means [two-toed amphiuma], and *Notophthalmus viridescens* [red-spotted newt]) on this ensemble of larval anurans. One other fish (*Esox americanus* [redfin pickerel]) and salamander (*Siren lacertina* [greater siren]) were found on NSGANW but were far less common and were not used in this study.

Most previous studies examining the effect of aquatic predatory vertebrates on larval anurans focused on the effect of *Notophthalmus* (Morin 1981, 1983, 1995, Wilbur et al. 1983, Wilbur 1987, Fauth 1990, Wilbur and Fauth 1990, Bristow 1991, Fauth and Resetarits 1991, Kurzava and Morin 1994, 1998). Four studies have compared *Notophthalmus* with one other aquatic predatory vertebrate (either *Ambystoma tigrinum*, *Ambystoma opacum*, *Enneacanthus obesus*, or *Siren intermedia*; Morin 1981, 1995, Fauth and Resetarits 1991, Kurzava and Morin 1998). Some comparisons suggested functional similarity between species while others suggested functional dissimilarity. Because of variation in prey species, abundances, and experimental conditions, the above experiments do not provide the framework necessary to compare the effects of species used in different studies.

METHODS

Experimental design

We evaluated how an ensemble of larval anurans responds to different predators by manipulating predator identity in replicated artificial ponds. Our experiment consisted of seven treatments; six treatments corresponding to the predator identities and the seventh treatment (control) representing absence of predators. We replicated each treatment four times in a randomized complete block design.

Field methods

We created a hexagonal array of 28 artificial ponds (1100-L Rubbermaid cattle watering tanks) in a large forest clearing at NSGANW in April 2000. Before the initiation of the experiment, we identified four clusters of seven ponds each as statistical blocks. Ponds within a block are closer together and should respond similarly to unknown spatial gradients. We conducted all procedures (e.g., creation of ponds, experimental manipulations, and monitoring of ponds) on a block-by-block basis to minimize variation within a block not attributable to treatment differences.

We filled artificial ponds on 13 April to a depth of 50 cm with water (volume: ≈1000 L) pumped from a nearby borrow-pit pond. A screen filter (mesh diameter: 2 mm) was placed over the pump intake to prevent transport of larval anurans or their predators into the artificial ponds. Zooplankton, periphyton, and phytoplankton could pass through the filter to serve as alternative prey base for the predators and as food for the larval anurans. Immediately after filling, we covered artificial ponds with a tight-fitting lid of fiberglass window screening to prevent unwanted colonizing by predatory insects and ovipositing by treefrogs, and to retain experimental organisms. On 14 April, we added 1 kg of leaf litter collected from the surrounding forest to each pond to create the same type of structural complexity and provide the same source of nutrients for the aquatic food web as in natural ponds. The following day we added a 500-mL mixture of zooplankton, periphyton, phytoplankton, and macroinvertebrates collected from a variety of ponds and ditches at NSGANW to supplement this complexity. We removed macroinvertebrates that could consume larval anurans from the mixture.

We added 175 newly hatched tadpoles of *Bufo, Rana*, and *Pseudacris* on 24 April to produce an initial density of 525 individuals/pond. These tadpoles were collected from four clutches of *Bufo*, six clutches of *Rana*, and 11 clutches of *Pseudacris*. Differences in the number of clutches used reflect differences in clutch size among species. Each pond received a similar fraction of newly hatched tadpoles from each clutch to ensure similar levels of genetic diversity among ponds. The following day we randomly assigned one of the seven treatments to each pond within a block. Predator treatments received two individuals of the designated species except *Amphiuma* ponds, which received one individual as a consequence of its lower natural density in comparison to the other predators. We ranked predators by size (within a species) and each block received predators of the same rank size. Initial body mass (mean ± 1 SE) of the predators used in this experiment was 4.542 ± 0.216 g (*Enneacanthus*), 0.207 ± 0.009 g (*Gambusia*), 2.963 ± 0.371 g (*Umbra*), 1.149 ± 0.029 g (*Ambystoma*), 128.305 ± 28.209 g (*Amphiuma*), and 2.117 ± 0.363 g (*Notophthalmus*). Although the natural modal density for any of these organisms may be higher or lower, the initial densities of all species fell within the range observed in natural ponds (Morin 1983, 1995, Harris et al. 1988, Bristow 1991; D. R. Chalcraft, *personal observation*). Using similar densities, however, allows us to evaluate similarity of individuals among different species. Additional studies are necessary to evaluate the conditions (i.e., relative population densities and biomasses) that generate functional similarity among predator populations (Chalcraft 2002; Chalcraft and Resetarits 2003).

We monitored ponds daily and collected anurans as they metamorphosed (defined as emergence of at least one forelimb). Metamorphs were weighed upon tail resorption. We recorded date of collection, metamorphosis, and wet mass (g) for each individual. Between 22 June and 25 June (duration of the experiment = 60–63 d) we drained all ponds and searched each thoroughly to produce a complete census of the surviving anurans and predators. Most surviving larvae had completed metamorphosis. We brought remaining individuals to the lab and recorded wet mass (g) of each.

Response variables and statistical analysis

We quantified the effect of each predator species on four response variables: importance, anuran species diversity, species composition, and survival. Importance was measured in terms of both total wet biomass (g) and total number of surviving larvae. Food web models (Hairston et al. 1960, Menge and Sutherland 1976, 1987, Fretwell 1977, Oksanen et al. 1981, McQueen et al. 1986, Ginzburg and Akçakaya 1992) suggest that as total biomass or total number increases so should the impact (and hence importance) of a guild on its food resources. We assayed both measures of anuran importance using MANOVA on $\log_{10}$-transformed data.

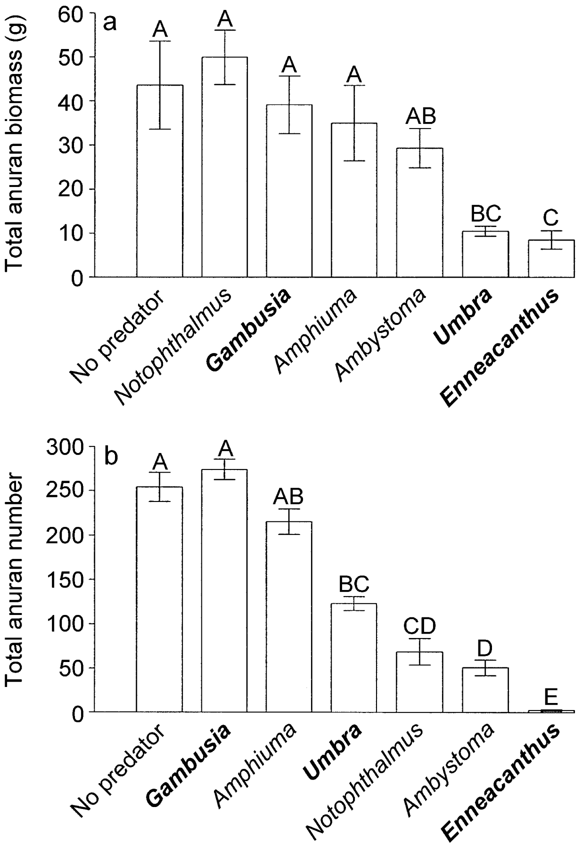

FIG. 1. Differences in ensemble importance among ponds with different top predators as represented by (a) mean total anuran biomass and (b) mean total anuran number (±1 SE). Uppercase letters above the bars identify pairs of means that are significantly different. Pairs of means were compared using Welsch's procedure. $N = 4$ in all cases. Fish are set in bold.

Indices of species diversity are typically comprised of two components: distribution of individuals among species (evenness) and number of species (richness) (Magurran 1988). We characterized both components of anuran species diversity using the Shannon index of species evenness and species richness (Magurran 1988) and used MANOVA on the response vector defined by evenness and richness. We defined ensemble composition using two vectors represented by the final relative abundances (p_i) and final relative biomasses (q_i) of each species. The final relative abundance or biomass of species i was the number or total biomass of individuals of species i surviving in a pond divided by the number or biomass of all anurans surviving in the same pond. Each vector provided an alternative measure of ensemble composition and we analyzed each with MANOVA to determine if composition was significantly different among ponds with different predators (Morin 1983). We arcsin transformed relative abundances and biomasses prior to analysis to remove linear dependence (i.e., the sum of transformed proportions in one pond

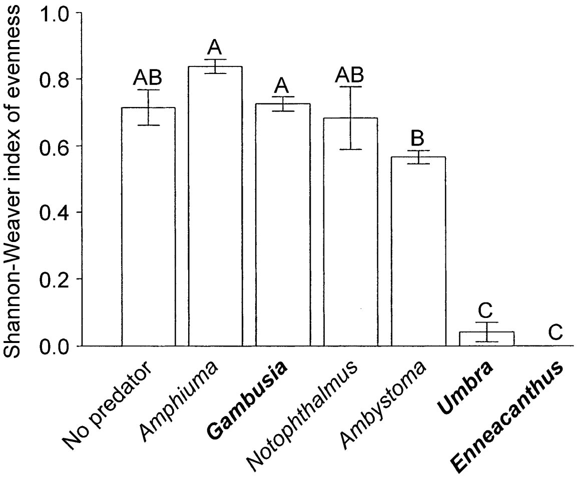

FIG. 2. Differences in ensemble species diversity among ponds with different top predators as represented by Shannon index of species evenness (±1 SE). Uppercase letters above bars identify pairs of means that are significantly different. Pairs of means were compared using Welsch's procedure. $N = 4$ in all cases. Fish are set in bold.

is not equal to the sum of transformed proportions in another). We measured probability of survival for each species as proportion of individuals (metamorphs and tadpoles) surviving, and analyzed survival using ANOVA. Survivorship values were arcsin transformed to homogenize variances.

Use of several MANOVAs to examine different logical subsets of the data is preferred to the use of a single MANOVA with all response variables, as large numbers of response variables dramatically reduce power (Scheiner 1993). Furthermore, the interpretation of MANOVAs conducted on subsets of data is more straightforward as all of the numbers in a response vector describe a single variable of interest (e.g., species diversity or composition). We used Pillai's trace as the criteria for significance tests because it is more robust than Wilks' lambda to small sample sizes and deviations from multivariate assumptions (Hair et al. 1995). Following any significant MANOVA, we conducted univariate ANOVAs on each component (e.g., species evenness and species richness) of the response vector (e.g., species diversity). This "protected ANOVA" is one solution to the problem of multiple statistical tests on different response variables (Scheiner 1993). Pairwise comparisons of means using Welsch's step-up test followed all univariate ANOVAs (Day and Quinn 1989) in order to determine which predators had significantly different effects while controlling type 1 error rates. We did not include total biomass of predators as a covariate because preliminary analyses indicated it was not correlated with any of our response variables.

RESULTS

Density of predators remained constant throughout the experiment with no predator mortality or recruitment. Predators differed in effects on both total anuran biomass (MANOVA predator effect, $F_{12,36} = 23.060$, $P < 0.001$; ANOVA predator effect, $F_{6,18} = 16.516$, $P < 0.001$) and total number of anurans (ANOVA predator effect, $F_{6,18} = 79.225$, $P < 0.001$). Different predators reduced total anuran biomass and number to differing extents (Fig. 1). Although *Enneacanthus* caused the greatest reduction in both biomass and number, rank position of other predators was different for each measure.

Predator treatments differed significantly in both species richness (MANOVA predator effect, $F_{12,36} = 7.285$, $P < 0.001$; ANOVA predator effect, $F_{6,18} = 18.375$, $P < 0.001$) and the Shannon index of evenness (ANOVA predator effect, $F_{6,18} = 57.296$, $P < 0.001$). Although rank positions of *Enneacanthus*, *Umbra*, and *Amphiuma* remained the same for evenness, rank position of the other three predators varied (Fig. 2). The pattern shown for richness was similar to that for evenness except that both *Ambystoma* and *Notophthalmus* had significantly different effects from all other predators, but did not differ from each other.

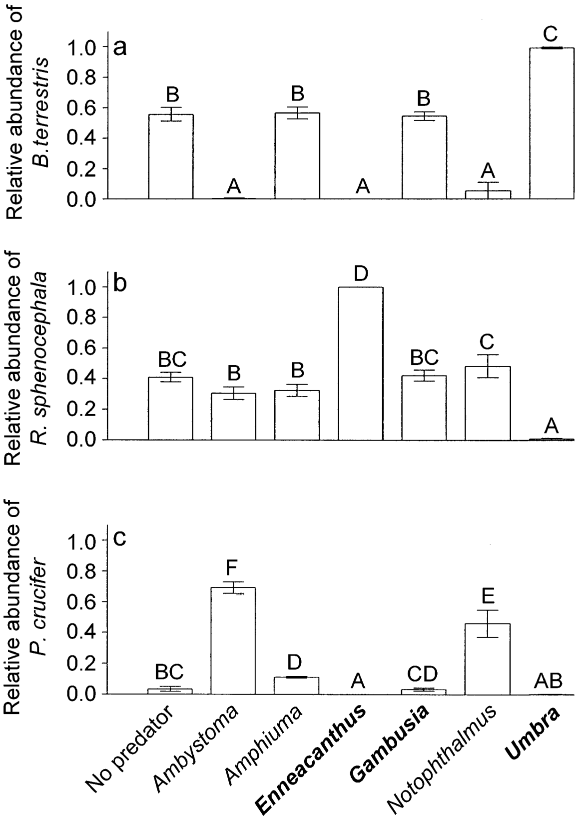

FIG. 3. Differences in the mean relative abundances of (a) *Bufo*, (b) *Rana*, and (c) *Pseudacris* among ponds with different top predators (±1 SE). Uppercase letters above the bars identify pairs of means that are significantly different. Pairs of means were compared using Welsch's procedure. $N = 4$ in all cases. Fish are set in bold.

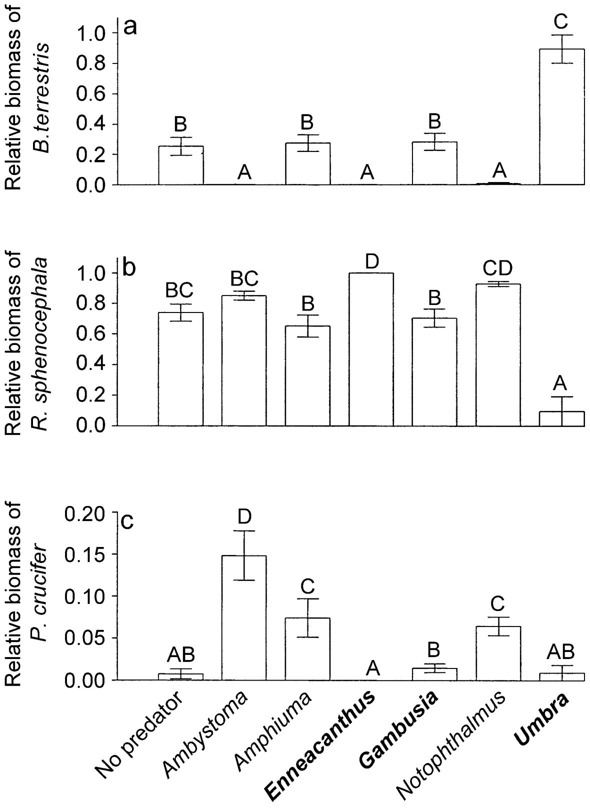

FIG. 4. Differences in mean relative biomass of (a) *Bufo*, (b) *Rana*, and (c) *Pseudacris* among ponds with different top predators (±1 SE). Uppercase letters above bars identify pairs of means that are significantly different. Pairs of means were compared using Welsch's procedure. $N = 4$ in all cases. Fish are set in bold.

Relative abundances of larval anurans were significantly different among treatments (MANOVA predator effect, $F_{18,54} = 19.643$, $P < 0.001$; *Bufo* ANOVA predator effect, $F_{6,18} = 95.406$, $P < 0.001$; *Rana* ANOVA predator effect, $F_{6,18} = 106.409$, $P < 0.001$; *Pseudacris*: ANOVA predator effect, $F_{6,18} = 66.667$, $P < 0.001$). Pairwise comparisons of relative abundances of the three prey species demonstrated a gradient of change as predator identity changed (Fig. 3).

Relative biomasses of larval anurans were also significantly different among treatments (MANOVA predator effect, $F_{18,54} = 19.657$, $P < 0.001$; *Bufo* ANOVA predator effect, $F_{6,18} = 40.556$, $P < 0.001$; *Rana* ANOVA predator effect, $F_{6,18} = 30.259$, $P < 0.001$; *Pseudacris* ANOVA predator effect, $F_{6,18} = 19.845$, $P < 0.001$). The pattern of prey relative biomass among predator treatments was different from the pattern of relative abundance. Pairwise differences in mean relative biomass again indicate a gradient of change across treatments (Fig. 4).

Survival probabilities for individual prey species were significantly different among treatments (*Bufo* ANOVA predator effect, $F_{6,18} = 138.007$, $P < 0.001$; *Rana* ANOVA predator effect, $F_{6,18} = 46.823$, $P < 0.001$; *Pseudacris* ANOVA predator effect, $F_{6,18} = 27.425$, $P < 0.001$). Although the survivorship of *Bufo* with different predators was typically either high or low, there was a continuum of change in both *Rana* and *Pseudacris* survival as predator identity changed (Fig. 5). Rank position of predators based on survivorship differed for each prey species.

DISCUSSION

Are top predators functionally similar?

Results demonstrate that for most common response variables, ranging from total anuran biomass to measures of individual species performance, our six predators of larval anurans were not functionally similar. Moreover, what similarity we did see depended on the particular response variable considered. Kurzava and Morin (1998) suggested that species will be functionally more similar when response variables are relatively coarse, aggregate measures (e.g., total mass or diversity

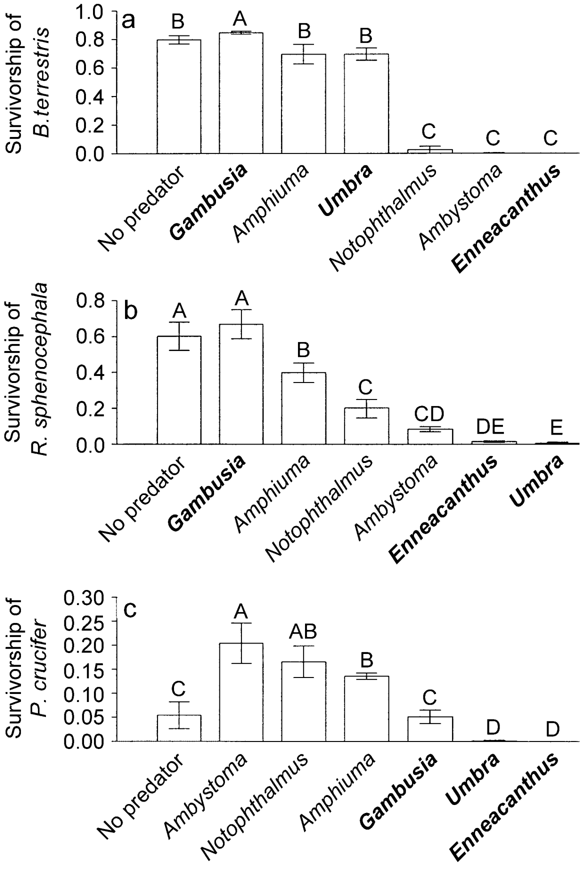

FIG. 5. Differences in survivorship of (a) *Bufo*, (b) *Rana*, and (c) *Pseudacris* among ponds with different top predators (±1 SE). Uppercase letters above bars identify pairs of means that are significantly different. Pairs of means were compared using Welsch's procedure. $N = 4$ in all cases. Fish are set in bold.

index of all prey species) as opposed to finely graded measures (e.g., total mass or relative abundance of individual prey species). In general, our data did show fewer significant differences among predators when the response variable was coarse (Figs. 1a, 2) and a greater number of significant differences when the response variable was fine (Figs. 3b,c, 4b,c, 5b,c). However, this pattern was far from universal, with a greater number of significant differences for one coarse measure (total anuran biomass, Fig. 1b) and fewer significant differences for several fine measures (Figs. 3a, 4a, 5a). This indicates that patterns of similarity across species are not simply determined by scale of resolution and suggests that there is no a priori justification for assuming that species will be more similar for certain response variables vs. others. While it is not overly surprising that our six predator species, representing six families in two classes, should have diverse impacts on a common set of prey, it is precisely this level of variation that is commonly overlooked when species are lumped. This has profound impacts on how we view biodiversity variation across natural landscapes, and how community structure and ecosystem function may respond to loss of species-level diversity (Petchey and Gaston 2002*a*). In a forthcoming paper, we evaluate how species traits such as gape size, microhabitat usage, and taxonomic affiliation contribute to producing differences in the effects of predators on their prey (Chalcraft and Resetarits 2003). It should be noted that functionally similar species may be more likely to occur in similar habitats when a wider geographic area is considered and it would be interesting to reveal what processes determine the scale at which functionally similar species co-occur.

Keystone predators and the selective landscape

Keystone predators play a pivotal role in natural communities. Their presence dramatically alters the structure of a community because they selectively consume competitively superior prey species and therefore alter the outcome of competitive interactions (Paine 1969). Several researchers (Morin 1981, 1983, 1995, Wilbur et al. 1983, Wilbur 1987, Fauth and Resetarits 1991, Kurzava and Morin 1998) have previously shown that predatory salamanders *Notophthalmus viridescens* and *Ambystoma opacum* alter the outcome of competitive interactions and hence relative abundance of prey species, thereby functioning as keystone predators. Our experiment confirmed this result, but another salamander in our study, *Amphiuma*, only demonstrated a weak keystone effect, slightly increasing survivorship and relative abundance of competitively inferior prey species (*Pseudacris*), probably by exerting a slightly stronger impact on a competitively dominant prey species (*Rana*). Unlike the other two salamanders, *Amphiuma* also caused a slight increase in species richness and evenness. Two fish predators, *Enneacanthus* and *Umbra*, also strongly affected the structure of the prey assemblage by increasing relative abundances of dominant competitors, either *Rana* or *Bufo*, and thereby reducing both species richness and evenness. The overall result of species turnover in the predator trophic position, however, was to produce a continuum of different larval anuran ensembles across ponds with different predators (Fig. 3). This is similar to the pattern described by Morin (1983) in which there was a continuum of larval anuran ensembles as density of *Notophthalmus* changed.

Evaluating the strength of interactions among species is a fundamental issue in community ecology (Laska and Wootton 1998), but very few studies have examined strength of interactions among a large number of species simultaneously. The studies that have been conducted (Paine 1992, Rafaelli and Hall 1992, 1996, Goldwasser and Roughgarden 1993, Fagan and Hurd 1994, de Ruiter et al. 1995, Wootton 1997, Gomez and Zamora 1999) suggest that most interactions between species are relatively weak. Many of these studies (Rafaelli and Hall 1992, 1996, Goldwasser and Roughgarden 1993, Fagan and Hurd 1994, de Ruiter et al. 1995), however, measured the strengths of interactions among groups of species rather than among individual species and some enhanced the number of interactions considered by examining the effects of a few predator species (≤3) on a wide array of prey groupings (11; Fagan and Hurd 1994) or prey species (23; Wootton 1997). Until our study, Paine's research (1992) had been the only study to measure the strength of interactions between a large number of species per se, manipulating the presence of seven consumer species and recording their effect on one prey species. In our experiment, we found a continuum in the impact of six predators on survivorship of two of their prey (*Rana* and *Pseudacris*), and predators had little similarity in their effects (Fig. 5b,c). For a third species (*Bufo*), the effects are dichotomous; either very strong effects or very weak effects (Fig. 5a). Regardless of the prey species considered, however, there was no predominance of weak interactors as in other studies (Fig. 5). Instead, predators appear evenly distributed along a gradient of interaction strength. We should also point out that the largest predator in our study was never the strongest interactor. Our results in conjunction with Paine's (1992) results support the assumptions and simulated results of Kokkoris et al. (1999); interaction strengths are distributed in a uniform manner at the regional scale but the process of community assembly causes interaction strengths to be distributed in a lognormal manner at the local scale. Obviously, more work is necessary to develop a better understanding of how interaction strengths are distributed within communities (Power et al. 1996, Wootton 1997).

Variation in the distribution of predators across regional landscapes will likely have a significant impact on population dynamics and evolution of prey species by producing variation in quality (in terms of prey survivorship and growth) of local breeding patches (i.e., ponds) (e.g., Levins 1970, Pulliam 1988, 1996, Thompson 1988, Gilpin and Hanski 1991, Hanski and Gilpin 1998). Simulation studies (Wilbur 1996, Alford and Richards 1999) and a long-term survey (Semlitsch et al. 1996) demonstrate that variation in recruitment of individuals from aquatic environments can have a significant impact on the dynamics of anuran populations. Given that our study shows that predators differ in effects on survival (see Chalcraft 2002 for differences in their effect on the growth of prey species) and that each predator often occurs in different ponds in our study area, differences in spatial distribution of predators across regional landscapes should impact anuran populations, as well as exert strong selective pressure. One consequence of such selection is clearly reflected in the avoidance of certain predators by ovipositing anurans (e.g., Resetarits and Wilbur 1989, Crump 1991, Petranka et al. 1994, Spieler and Linsenmair 1997, Summers 1999, Binckley and Resetarits 2002). Certainly the degree to which ovipositing anurans avoid different predators should be related, at least in part, to the degree that predators differ in their effects on larval performance.

Conceptual models for the distribution of predators across landscapes often emphasize differences in their physiological tolerances (Wellborn et al. 1996, Skelly 1997). Not considered, however, is temporal variation in predator distributions resulting from both climatic variation and dispersal capabilities. Gill (1978) has demonstrated substantial movement of *Notophthalmus* among ponds, and intermittent connectivity between patches allows dispersal of fish species (Sexton and Phillips 1986, Magnuson et al. 1998, Matthews and Robison 1998, Eason and Fauth 2001, Olden et al. 2001), even into newly formed ponds (*personal observations*). Thus, depending on frequency of dispersal among patches and patch permanence, predators within a given pond may vary from year to year or even within a given year. Such variation is of little consequence if predators are functionally similar, but may be profound if predators differ in their functional role.

Functional similarity and ecological theory

The idea that communities consist of groups of functionally similar species is a pervasive assumption underlying studies of complex interactions in both community and ecosystem ecology (Martinez 1991, Polis 1991). Most theories of trophic interactions predict that predators should reduce number and biomass of their prey (see Leibold 1989, 1996 for exception). This prediction was only weakly supported by this study; only three of six predators reduced total anuran biomass, while five of six reduced total anuran number (Fig. 1). Furthermore, extent of reduction in both total anuran number and total anuran biomass was different for each predator, and rank order differed for the two response variables. Our results may deviate from predictions for two reasons. First, food web theory (e.g., Hairston et al. 1960, Menge and Sutherland 1976, 1987, Fretwell 1977, Oksanen et al. 1981, McQueen et al. 1986, Ginzberg and Akçakaya 1992) does not readily account for differences among predators in their ability to reduce number and biomass of prey. Second, reductions in total prey biomass may not match reduction in total prey number because of compensatory growth by survivors. Extent of compensation depends upon differences in the tolerance of prey to competitive environments and differences in maximum size at metamorphosis. In our system, *Bufo* was most tolerant of competition and *Pseudacris* least tolerant (Morin 1981, 1983, Wilbur et al. 1983, Wilbur 1987, Fauth and Resetarits 1991, Chalcraft 2002). *Rana* was largest at metamorphosis and *Bufo* smallest (Chalcraft 2002). Therefore, even though total number of anurans with *Gambusia* was significantly greater than with *Notophthalmus*, there was no significant difference in biomass because of reduced competition and a shift to larger bodied species with *Notophthalmus*. Of course, ability of prey species to compensate for reductions depends on their survival prospects. For example, total anuran biomass with *Enneacanthus* was lower than in ponds with other predators despite the virtual absence of competitive interactions and the presence of large bodied species, simply because so few individuals survived.

Leibold's keystone predation model (Leibold 1989, 1996) represented a significant step in the development of food web theory that accounted for differences in species responses within trophic levels. Our results support this model in that relative strength of ‘‘top-down’’ effects depended upon species turnover within the food web. Leibold's model, however, emphasized the importance of compositional turnover among prey associated with changes in nutrient supply. In our experiment, nutrient supply did not vary; predators may have affected nutrient turnover rate but not total supply because no predators died. So, although there is growing support for Leibold's model (Leibold 1996), a nutrient gradient is not necessary to produce variation in relative intensity of top-down effects. Instead, a gradient of interaction strengths associated with changes in predators produced variation in relative intensity of top-down effects.

In addition to being an assumption of much food web theory, functional similarity is frequently argued to be a mechanism responsible for the relationship between biodiversity and community or ecosystem stability and function (e.g., McNaughton 1977, Naeem and Li 1997, Naeem 1998, Yachi and Loreau 1999). Some authors have proposed that as biodiversity increases so does the occurrence of species that are functionally similar, and it is this redundancy that provides insurance against loss or degradation of critical processes (Elton 1958, Walker 1991). It has also been argued that it is important to maintain redundancy both among and within local communities because species that are redundant in effect will not necessarily be redundant in responses to environmental change (Wellnitz and Poff 2001). While both points are logically compelling, our data suggest that, at least at higher trophic levels, functional redundancy of effects may be rare. Given that we could typically distinguish the effects of different predators on several different response variables, it seems unwise to consider them functionally redundant (Harris 1995). However, the continuum of functional effects indicates that certain species are more similar (though not redundant). This indicates that these predators are neither equally unique nor are they redundant. Hence, each species plays a different functional role but the extent of change associated with predator loss or replacement will depend on the species.

CONCLUSIONS

Variation in species composition of predators can have important consequences for food webs. Although ecologists have recognized spatial and temporal changes in species composition within local communities, we have fallen into a practice of overlooking the importance of this variation by assuming that species occupying similar trophic positions act in a similar manner. This presumed similarity, however, is simply not in evidence among predators of larval anurans. Therefore, loss of any of these predators from the regional landscape would constitute loss of a functional role. This is of particular concern given the well-documented importance of top-down control of community structure in many systems (Brett and Goldman 1997, Resetarits and Fauth 1998, Polis 1999, Chase 2000), and the fact that local and global extinctions are more likely for species occupying higher trophic levels within food webs than for species at lower trophic levels (Petchey et al. 1999, Pounds et al. 1999). If similarity of effects is indeed rare in ecological communities, any relationship between biological diversity and community or ecosystem processes may be driven not by functional redundancy, but rather by a diversity of species having different functional roles. Under this scenario, losses in species diversity constitute real losses of functional roles, and may constrain community and ecosystem processes.

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