

Functional diversity of non-lethal effects, chemical camouflage, and variation in fish avoidance in colonizing beetles

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Abstract. Predators play an extremely important role in natural communities. In freshwater systems, fish can dominate sorting both at the colonization and post-colonization stage. Specifically, for many colonizing species, fish can have non-lethal, direct effects that exceed the lethal direct effects of predation. Functionally diverse fish species with a range of predatory capabilities have previously been observed to elicit functionally equivalent responses on oviposition in tree frogs. We tested this hypothesis of functional equivalence of non-lethal effects for four predatory fish species, using naturally colonizing populations of aquatic beetles. Among taxa other than mosquitoes, and with the exception of the chemically camouflaged pirate perch, *Aphredoderus sayanus*, we provide the first evidence of variation in colonization or oviposition responses to different fish species. Focusing on total abundance, *Fundulus chrysotus*, a gape-limited, surface-feeding fish, elicited unique responses among colonizing Hydrophilidae, with the exception of the smallest and most abundant taxa, *Paracymus*, while Dytiscidae responded similarly to all avoided fish. Neither family responded to *A. sayanus*. Analysis of species richness and multivariate characterization of the beetle assemblages for the four fish species and controls revealed additional variation among the three avoided species and confirmed that chemical camouflage in *A. sayanus* results in assemblages essentially identical to fishless controls. The origin of this variation in beetle responses to different fish is unknown, but may involve variation in cue sensitivity, different behavioral algorithms, or differential responses to species-specific fish cues. The identity of fish species occupying aquatic habitats is crucial to understanding community structure, as varying strengths of lethal and non-lethal effects, as well as their interaction, create complex landscapes of predator effects and challenge the notion of functional equivalence.

Key words: beetles; chemical camouflage; community assembly; diversity; fish; functional diversity; functional equivalence; functional redundancy; habitat selection; non-lethal effects; predation; species turnover

INTRODUCTION

The question of whether species occupying the same guild or taxon have similar functions within natural communities is a longstanding debate in ecology (Lawton and Brown 1993, Kurzava and Morin 1998, Chalcraft and Resetarits 2003a,b, Loreau 2004, Resetarits and Chalcraft 2007, Losos 2008, Thibault et al. 2010, Rudolf et al. 2014, Hussey et al. 2015, Michalko and Pekar 2016). Functional equivalence vs. functional diversity of ecological roles, both within communities and on a regional scale, have vastly different implications for species conservation and preservation of community and ecosystem function (Petchey and Gaston 2006, Resetarits and Chalcraft 2007). Functional equivalence carries a variety of meanings, from equivalence in effects on communities to equivalence in response to environmental variation (including species composition).

The more important the ecological role in a community, the more critical the distinction between functional equivalence and functional diversity. Predators

play an important role in marine, freshwater, and terrestrial systems (Paine 1966, Kerfoot and Sih 1987, Wellborn et al. 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Estes et al. 2011), but they may be especially important in freshwater lentic communities owing to the closed, discrete nature of the communities, where predators and prey are constrained to a specific habitat patch (pond, lake) for their entire life, or the duration of the aquatic stage in amphibious complex life cycles (Morin 1983, Wellborn et al. 1996, Wilbur 1997).

Predator impacts include both lethal and non-lethal effects, with lethal effects being historically viewed as primary determinants of community structure, and non-lethal effects driving more subtle aspects of prey habitat use and performance (but see Lima 1998, 2009, Preisser et al. 2005, Ale and Whelan 2008, Orrock et al. 2008, Peckarsky et al. 2008). However, habitat selection, a specific form of non-lethal direct effect, can have profound impacts on species distributions and community structure in aquatic systems (Resetarits and Wilbur 1989, Blaustein 1999, Resetarits 2005, Resetarits and Binckley 2009, Vonesh et al. 2009, Kraus and Vonesh 2010, Resetarits and Silberbush 2016). The idea that predators affect the distribution and abundance of prey species without “face

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to face” interactions has given rise to the idea of phantom interactions (Resetarits et al. 2005), which then generate remote effects (Orrock et al. 2010).

A large proportion of freshwater fauna consists of larval and adult stages of organisms with complex life cycles. These are primarily terrestrial as adults (e.g., amphibians, dipterans, odonates), or must leave the water at some point to complete their life cycle (e.g., aquatic beetles–terrestrial pupation: Merritt and Cummins 1984, Duellman and Trueb 1986, Hutchinson 1993, Schneider and Frost 1996, Wilbur 1997). Persistence is dependent on recurrent immigration in the form of colonization and/or oviposition by dispersing adults. Freshwater aquatic landscapes are thus comprised of patches (communities) linked to each other (as metacommunities), and to the surrounding terrestrial matrix, largely by species with complex life cycles. Thus, immigration, and processes that drive immigration, play a particularly critical role in the ongoing process of community assembly.

The transition from fish to fishless habitats is a defining characteristic for freshwater communities (Wellborn et al. 1996). Thus, many colonizing aquatic organisms (whether immigrating or ovipositing) recognize and actively avoid habitats containing fish (Binckley and Resetarits 2003, 2005). While even closely related fish may differ in their actual effects on aquatic communities (Resetarits and Chalcraft 2007), colonizers such as amphibians and aquatic insects show similar levels of avoidance of fish ranging from small planktivores, such as *Pimephales promelas* and *Notemigonus crysoleucas*, to larger, voracious predators such as *Esox* and *Lepomis*, (Binckley and Resetarits 2003, Resetarits and Binckley 2013). The only clear exception is the pirate perch, *Aphredoderus sayanus*, which is chemically camouflaged (Resetarits and Binckley 2013). It is surprising, however, that colonizing organisms fail to discriminate among fish with such different predatory effects. Only the mosquito *Culex restuans* (Culicidae) has been shown to discriminate on a finer scale among fish species (Eveland et al. 2016; W. J. Resetarits, *unpublished data*), but whether this involves species-specific recognition, and is actually adaptive, remains undetermined.

For the dominant families of aquatic beetles (Dytiscidae and Hydrophilidae), larvae and adults are obligately aquatic, thus adults choose a habitat both for themselves and their offspring. Dispersal flights are energetically costly, and limited evidence suggests that, once initial settlement is complete, beetles rarely undergo secondary dispersal unless conditions change dramatically (e.g. pond drying: Zalom et al. 1979, Layton and Voshell 1991, Sheldon 1992, Jeffries 1994, Bilton 2014). This partly derives from the fact that individuals (especially females) of some species histolyse flight muscles to fuel reproduction and/or development of swimming muscles (Johnson 1969, Zera and Denno 1997). Thus, initial colonization decisions are critical, and we would expect colonizing beetles to discriminate among fish species based on expected predatory impact.

Given that predators can maintain, enhance, or degrade biodiversity, determining functional roles and the extent of functional equivalence is critical to understanding and protecting ecological communities (Prugh et al. 2009, Estes et al. 2011). A functionally diverse set of fish with a range of predatory capabilities elicit largely functionally equivalent responses for oviposition rate in treefrogs (Binckley and Resetarits 2003, Resetarits and Binckley 2013). We conducted a field experiment to test this hypothesis of functional equivalence of non-lethal effects, examining the responses of naturally colonizing aquatic beetles to four species of predatory fish (see *Materials and Methods*) that vary in taxonomic position, habitat, and morphology, and are among the most abundant at our field site.

MATERIALS AND METHODS

We conducted a mesocosm field experiment in a naturally colonized experimental landscape at the University of Mississippi Field Station (UMFS), during May and June 2015. UMFS consists of 318 ha containing a mix of oldfields, forest, streams, and natural and experimental wetlands located within the Eocene Hills of the Interior Coastal Plain in Lafayette County, Mississippi. The forest is mixed shortleaf pine and oak along with loblolly pine, sweet gum, black gum, winged elm, and red maple.

Our experiment was set up using artificial pools in a linear arrangement of five spatial blocks of five pools each ($N = 25$), spaced >2 m apart near the oldfield/forest ecotone. We used children’s wading pools, (1.50 m diameter \times 0.29 m deep, holding c. 300 L) as colonization pools. Pools were placed 0.67 m apart within a block, filled with well water and 0.5 kg of dry, predominately hardwood, leaf litter from the surrounding forest, covered with oversize screen lids (1.3 \times 1.13 mm mesh), and allowed to age for 7 d. Randomized aliquots of zooplankton and phytoplankton were added on 29 April and fish were added on 1 May. Treatments consisted of addition of one of four fish species, plus fishless controls, replicated once within each of five blocks. Fish species (no./pool) were pirate perch, *Aphredoderus sayanus* (AS) (2); golden topminnow, *Fundulus chrysotus* (FC)(3); green sunfish, *Lepomis cyanellus* (LC)(1); and longear sunfish, *L. megalotis* (LM)(1). Size and number per pool varied as a result of variation in species body size and availability in the natural ponds (see *Results*). We randomly added individuals of the different species, matching biomass as much as possible within blocks, while maintaining reasonable densities. Certain species, notably *Fundulus chrysotus*, are intraspecifically aggressive and can cause mortality at high densities, so we were conservative in our approach, which resulted in 100% survival for 48 d of the experiment. Prior research has suggested that colonization/oviposition responses to fish involve thresholds at quite low densities, and all of our densities exceeded that threshold (Resetarits and Binckley 2013).

These four fish are among the most common species at UMFS, and provide contrasts in phylogeny, morphology,

habitat use, and predatory potential. All four species are either good dispersers or can persist in semi-ephemeral habitats. The pirate perch, *Aphredoderus sayanus*, is a benthic, nocturnal predator, unique both phylogenetically and morphologically, and is known to generate no responses from colonizing beetles, ovipositing treefrogs, or *Culex* mosquitoes (A. Silberbush and W. J. Resetarits, *Unpublished manuscript*, Resetarits and Binckley 2013). The longear sunfish, *Lepomis megalotis*, has been previously shown to repel beetles (Resetarits 2001), while the green sunfish, *L. cyanellus*, has not previously been tested with beetles, but do not repel *Culex* (A. Silberbush and W. J. Resetarits, *Unpublished manuscript*). Both *Lepomis* feed at all depth levels in ponds. *Lepomis cyanellus* is also one of the most widespread fishes in North America and is widely introduced to previously fishless waters both inside and outside of its native range (Lee et al. 1980). The golden topminnow, *Fundulus chrysotus*, is a small, surface-feeding, gape-limited fish that has not been previously tested with beetles, but generates the strongest response from *Culex* among over 30 fish species tested (W. J. Resetarits, *unpublished data*) and provides a contrast in morphology, habitat use, and predatory potential.

It should be noted that distances between pools were within the range over which spatial contagion has been observed (Binckley and Resetarits 2009), so our results should be viewed as a conservative estimate of fish effects and differences among fish. Fish effects have been clearly observed in numerous previous experiments with similar interpool distances, where all spatial blocks have the same treatments represented. The latter seems to obviate or at least minimize the effects of contagion (Binckley and Resetarits 2005).

On 3 May, we submerged screen lids under water to separate fish (who remain under the screens) from colonists. This prevents any direct contact/harassment/consumption of target species, but allows passage of chemical cues that can be detected by organisms assessing ponds for colonization/oviposition, and allows complete assay of all but the very smallest beetles. We collected all adult beetles every 4 d without replacement until 17 June, resulting in 11 samples/pool. One pool (5-1; *L. megalotis*) failed (drained) on 8 June, resulting in only nine samples; this had no impact on the results, so no adjustment was made to the data. Beetles were preserved in ethanol and identified to species. Because all colonists above were removed from above the screens every 4 d, we effectively retarded development of the community such that the colonization landscape was relatively constant across the experiment. Only zooplankton, phytoplankton, and species that could pass through the screen mesh, such as chironomids, other very small dipterans, and some tiny beetles, were able to colonize the water below the screens.

Data analysis

We conducted a MANOVA on the number of dytiscids and hydrophilids (excluding *Paracymus*) per pool, and individual univariate ANOVAs for each family. Temporal

patterns in the data reflected seasonal activity of beetles, so aggregate samples were appropriate. Because of its abundance (3240 individuals), very small size, and the difficulties inherent in identification, we conducted a separate univariate ANOVA for *Paracymus*, which was the only beetle taxa in which not all individuals were identified to species (95% of those identified were *P. subcupreus*, and the rest that were identified were *P. confusus*). We also conducted an ANCOVA on overall beetle species richness with abundances as the covariate, and individual ANOVAs for the next seven most abundant species (all species with >100 individuals). Treatment means were compared using Fisher's Protected LSD following main effects with $P < 0.10$; we retained a critical value of 0.05 for individual comparisons. We used a blocked PERMANOVA focusing on the Bray-Curtis Index, including both abundance and species composition, to test whether differences in mean community composition (i.e., differences in multivariate location per treatment) differed among treatments, and visualized this using nonmetric multidimensional scaling (NMDS). We further examined the data by analyzing presence-absence dissimilarity using both Bray-Curtis and Jaccard, examining the correlation (Pearson's product moment) between abundance of dytiscids and hydrophilids, and conducting regression on the relationship between fish mass and beetle abundance, as well as on the relationship between beetle abundance and species richness. MANOVA/ANOVA analyses used SAS v. 9.3 (SAS Institute, Cary, North Carolina, USA) with Type III sums of squares and $\alpha = 0.05$, regression and correlation was done in SigmaPlot v.11.0 (Systat Software, San Jose, California, USA). PERMANOVA and NMDS plots used PRIMER 7 with PERMANOVA add-on (PRIMER-E, Plymouth, UK).

RESULTS

Our experiment was colonized by 5,240 individuals of 44 species of aquatic beetles (Table 1); 1,413 individuals of 24 species (15 genera) of Dytiscidae, 3,750 individuals of 16 species (six genera) of Hydrophilidae (including 3240 *Paracymus*), 22 individuals of three species (two genera) of Haliplidae, and 40 individuals of a single species of Helophoridae. Non-beetle taxa in our samples were *Limnoporus canaliculatus* (Gerridae; 4), *Hesperocorixa* (Corixidae; 9), *Notonecta irrorata* (Notonectidae; 12), *Sigara* (18), and numerous eggs of Cope's gray treefrog, *Hyla chrysoscelis* (which were removed the following morning).

Abundance

Collectively beetles colonized all fish treatments, with the exception of AS, at significantly reduced rates (Table 2a, Fig. 1a). Dytiscids also strongly avoided all species of fish, with the exception of AS, which was not significantly different from controls (Table 2b, Fig. 1b). For hydrophilids (without *Paracymus*), LC and LM, but not AS and FC, were significantly different from controls (Table 2c, Fig. 1b). *Paracymus* responses were the same

TABLE 1. Species and abundances for colonizing beetles (total number of species = 44, $N = 5240$).

Species	Abundance
Dytiscidae	
<i>Acilius mediatus</i>	2
<i>Celina imitatrix</i>	1
<i>Copelatus chevrolati</i>	3
<i>Copelatus glyphicus</i>	410
<i>Desmopachria convexa</i>	4
<i>Hydrocolus deflatus</i>	5
<i>Hydrocolus oblitus</i>	3
<i>Hydroporus pseudoniger</i>	5
<i>Hydroporus niger</i>	121
<i>Hydrovatus pustulatus</i>	1
<i>Ilybius biguttulus</i>	2
<i>Laccophilus fasciatus</i>	299
<i>Laccophilus maculosus</i>	3
<i>Laccophilus proximus</i>	327
<i>Neobidessus pullus</i>	1
<i>Neoporus blanchardi</i>	1
<i>Neoporus undulatus</i>	2
<i>Platambus astrictovittatus</i>	1
<i>Prodaticus bimarginatus</i>	1
<i>Rhantus calidus</i>	1
<i>Thermonectus basillaris</i>	3
<i>Thermonectus nigrofasciatus</i>	1
<i>Uvarus granarius</i>	201
<i>Uvarus lacustris</i>	15
Hydrophilidae	
<i>Berosus exiguus</i>	15
<i>Berosus infuscatus</i>	44
<i>Berosus peregrinus</i>	5
<i>Berosus pugnax</i>	1
<i>Berosus striatus</i>	2
<i>Cymbiodyta chamberlaini</i>	3
<i>Enochrus consors</i>	3
<i>Enochrus hamiltoni</i>	1
<i>Enochrus ochraceus</i>	103
<i>Enochrus perplexus</i>	9
<i>Enochrus pygmaeus</i>	25
<i>Helochaers maculicollis</i>	20
<i>Paracymus</i>	3,240
<i>Tropisternus blatchleyi</i>	4
<i>Tropisternus collaris</i>	35
<i>Tropisternus lateralis</i>	255
Haliplidae	
<i>Haliplus triopsis</i>	2
<i>Peltodytes muticus</i>	18
<i>Peltodytes litoralis</i>	2
Helophoridae	
<i>Helophorus linearis</i>	40

as for dytiscids, with all species avoided except AS (Table 2d, Fig. 1c).

Species richness per patch ranged from 6 to 20 species. Abundance explained 45% of the variation in species richness, but treatment was also significant and explained

an additional 29% (Table 1e, Fig. 1d). Richness was significantly reduced by all species of fish except AS. Among avoided species, LC had significantly lower species richness than FC, while LM was intermediate and not significantly different from the other two (Fig. 1d). The richness–abundance relationship showed a classic, non-linear, saturating curve, with saturation occurring at ≈ 17 species (Fig. 2a). The overall similarity in responses is reflected in the significant positive relationship between the abundances of dytiscids and hydrophilids, even with the exclusion of *Paracymus* (whose responses precisely mirror the dytiscids; $r = 0.844$, $df = 24$, $P < 0.0001$, Fig 2b). The exception is the non-*Paracymus* hydrophilid responses to FC, which generates points largely off the regression line. Because of variation in size and availability, there were large differences in fish biomass among species, however, abundance for all beetles (shown), non-*Paracymus* hydrophilids, dytiscids, and *Paracymus* (not shown) all show no effect of total fish biomass/pool either among or within avoided species (AS excluded; $R^2 = 0.0032$, $F_{1,13} = 0.0420$, $P = 0.841$, Fig. 2c). The complete lack of response by beetles to AS has since been confirmed at densities over twice what we used in this experiment (W. J. Resetarits, unpublished data).

Including *Paracymus*, none of the eight most abundant species avoided AS, and one species, *Uvarus granarius*, had significantly greater abundance with AS than controls (Fig. 3). FC, LC, and LM were all significantly lower than controls for five species: *Paracymus*, *Copelatus glyphicus*, *Laccophilus proximus*, *U. granarius*, and *Hydroporus niger*. For two others, *L. fasciatus* and *Tropisternus lateralis*, FC was not significantly different from controls, while there were no differences among treatments for *Enochrus ochraceus* (Fig. 3).

Assemblage structure

Examining the structure and composition of beetle assemblages in plots with avoided fish (LC, LM, FC) vs. control + AS treatments, we find virtually no overlap in the NMDS plots (Fig. 4a). By treatment, assemblages of colonizing beetles were also significantly different (Table 3a, Fig. 4b). The NMDS plot suggests three different clusters, with C and AS largely overlapping, LM and LC overlapping to a lesser degree, and FC clustering by itself. PERMANOVA results largely conform with the NMDS plots. For all beetles, the greatest similarity among replicates, within treatments, occurred in AS patches (71.93), while the lowest similarity occurred among LM patches (52.51). Among treatments, AS and C were most similar (66.00) and not significantly different, while LC and AS showed the greatest dissimilarity (41.89). All three avoided fish treatments were significantly different from both Controls and AS, while only LC and FC were significantly different among avoided fish (Table 3a, Fig. 4b). Thus, the NMDS plots place AS almost entirely within the polygon defined by control plots, and AS had the greatest internal similarity of any

TABLE 2. ANOVAs for primary responses. Significant effects in bold.

	df	SS	MS	F	Pr > F
(a) All beetles					
Block	4,16	107.07	26.77	8.81	0.0006
Fish species	4,16	163.14	40.78	13.42	<0.0001
(b) Dytiscidae					
Block	4,16	76.39	19.10	11.74	0.0001
Fish species	4,16	112.95	28.24	17.36	<0.0001
(c) Hydrophilidae (w/o <i>Paracymus</i>)					
Block	4,16	32.94	8.23	3.73	0.0249
Fish species	4,16	60.92	15.23	6.91	0.0020
(d) <i>Paracymus</i>					
Block	4,16	257.28	64.32	2.69	0.0688
Fish species	4,16	758.11	189.53	7.93	0.0010
(e) Species richness (all beetles)					
Abundance	1,15	159.54	159.54	32.99	0.0001
Block	4,15	36.68	9.17	1.90	0.1635
Fish species	4,15	103.22	25.81	5.34	0.0071

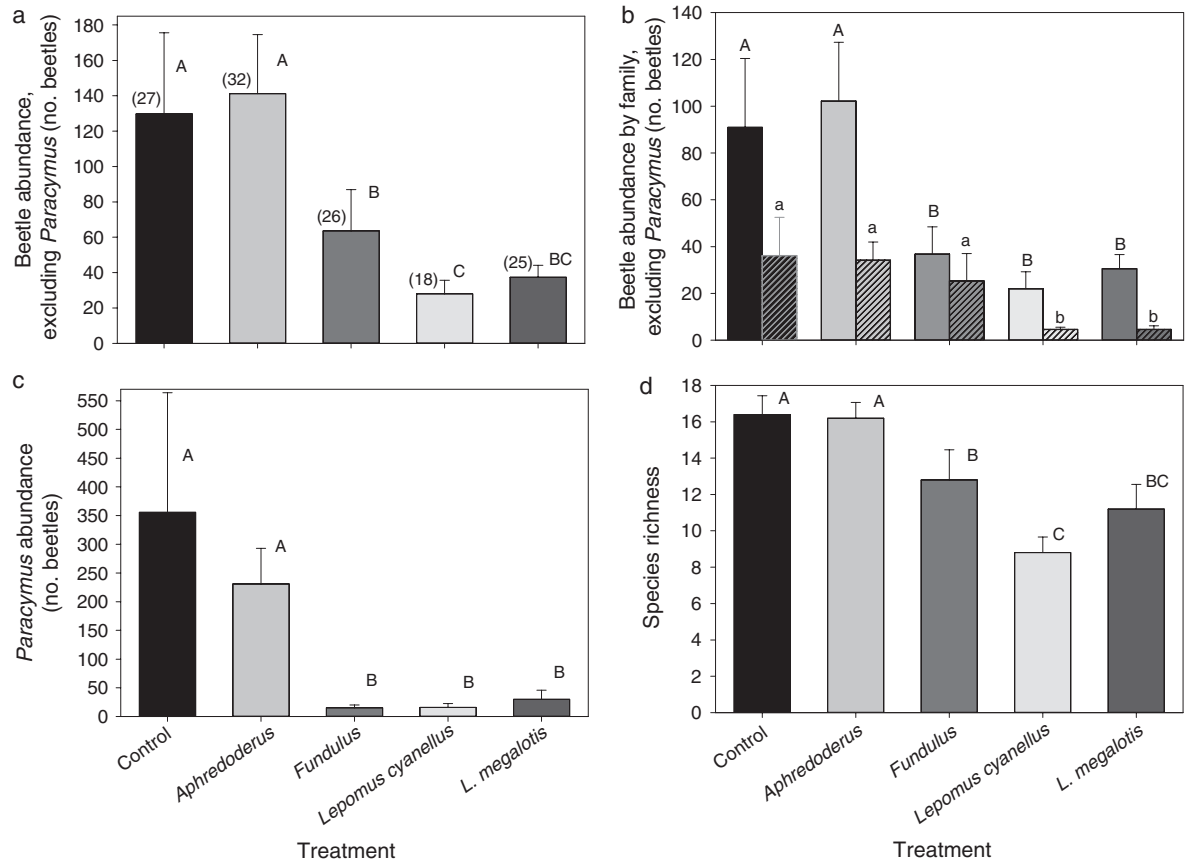


FIG. 1. (a) Abundance of all colonizing beetles (excluding *Paracymus*) in the five treatments. Numbers in parentheses are total number of beetle species represented in that treatment (including *Paracymus*). (b) Abundance by family, Solid bars, Dytiscidae; hatched bars, Hydrophilidae (without *Paracymus*). (c) Abundance of *Paracymus* in the five treatments. (d) Species richness of beetles in the five treatments. All panels show mean + SE. Different letters above bars indicate significantly different treatments ($P < 0.05$); in panel b, uppercase letters indicate dytiscids, lowercase hydrophilids.

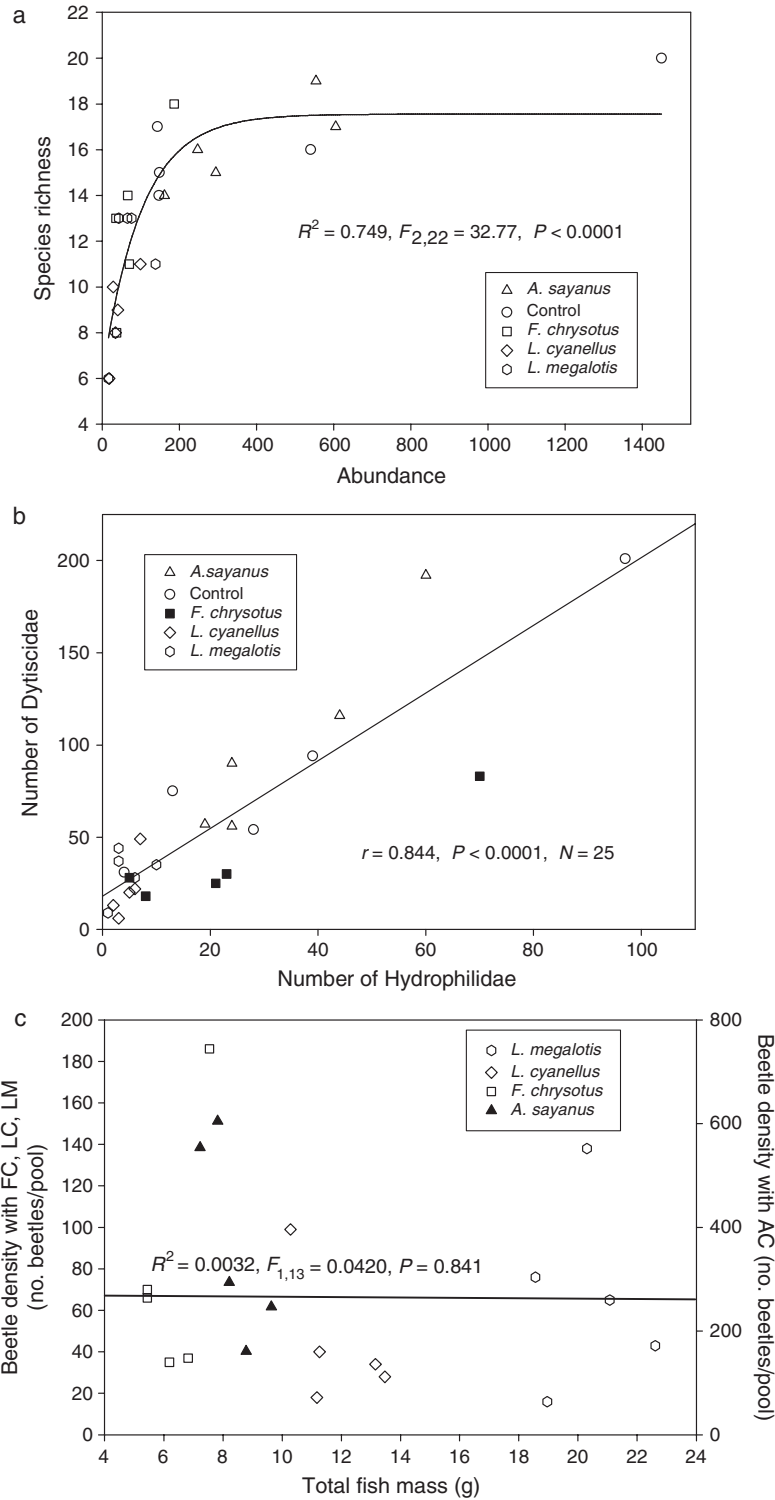


FIG. 2. (a) Species abundance curve for beetles shows classic saturating curve. (b) Correlation between the number of dytiscids and hydrophilids in individual pools in the experiment. There is overall similarity in responses (excepting the lack of response by hydrophilids to *Fundulus* [solid symbols]), and no evidence of mutual avoidance between the two families. (c) Regression plot of beetle abundance per pool vs. fish biomass. Regression line and equation excludes *A. sayanus* (solid symbols) and illustrates lack of effect of biomass across avoided fish species. Note different scale (4 \times) for AS (right hand axis). Within species: FC $R^2 = 0.3566, F_{1,4} = 1.66, P = 0.2874$; LC $R^2 = 0.3582, F_{1,4} = 1.67, P = 0.2863$; LM $R^2 = 0.0002, F_{1,4} = 0.0006, P = 0.9817$. Fish species were pirate perch, *Aphredoderus sayanus* (AS); golden topminnow, *Fundulus chrysotus* (FC); green sunfish, *Lepomis cyanellus* (LC); and longear sunfish, *L. megalotis* (LM).

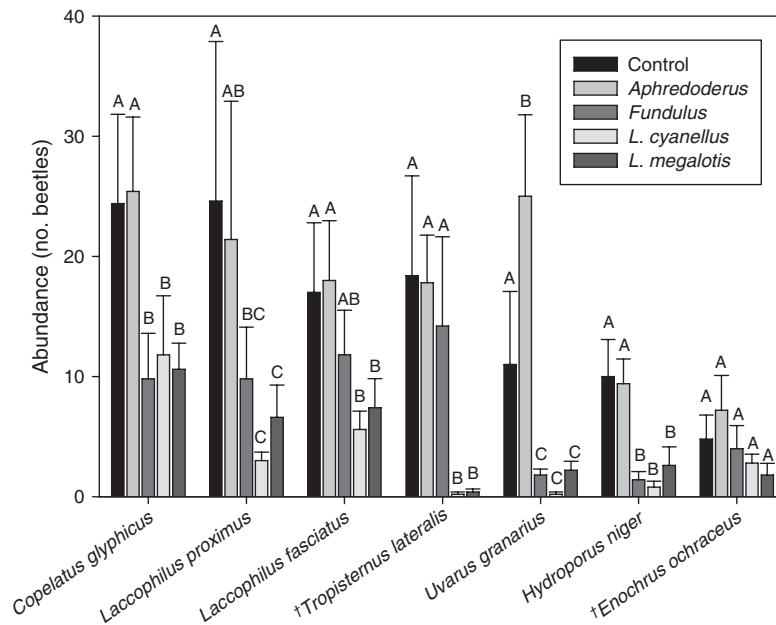


FIG. 3. Abundance (mean + SE) of the next seven most-abundant species (after *Paracymus*) in the five treatments. Different letters indicate treatments significantly different within each beetle species ($P < 0.05$). † Hydrophilidae.

treatment, including controls, while FC generates unique assemblages for all beetles, and hydrophilids excluding *Paracymus*, and there is greater overlap between the two *Lepomis* species for dytiscids (Table 3, Fig. 4). Removal of *Paracymus* from the hydrophilids increases overlap of FC with control and AS treatments (not shown), reflecting the overall pattern for abundance and species richness.

A total of 14 species were shared by all five treatments, and there were 13 species found in only a single treatment: three each for three fish treatments, none for LC, and four for the controls. Each of the unique species except one (four individuals) were represented by one or two individuals. Nine species were found only in the un-avoided treatments (C + AS), and seven only in the avoided fish treatments; only one of those in either group had more than a few individuals, *Berosus exiguus*, which had 15 individuals between C and AS (Table 1). Cumulative total richness was highest for AS pools (32 species), while C, FC, and LM had similar total richness (27, 26, 25, respectively) with LC considerably lower, represented by only 18 species (Fig. 1a).

Examining composition of assemblages by family, dytiscids were also significantly different among treatments (Table 3b, Fig. 4c), and reflect the overall pattern for all beetles. The NMDS plot suggests the treatments largely form two clusters, with avoided fish forming one group of loosely overlapping clouds, while C and AS strongly overlap. PERMANOVA results again largely conform with the NMDS plots. For dytiscids, the greatest similarity among replicates, within treatments, again occurred in the AS patches (72.63), while the lowest similarity occurred among the LM patches (61.64). AS and C

treatments were the most similar (68.72) and not significantly different, while LC and C and LC and AS showed the greatest dissimilarity (49.25, 49.56 respectively). All three avoided fish treatments were significantly different from controls and AS, but not from one another (Table 3b, Fig. 4c).

Composition of assemblages of colonizing hydrophilids also differed significantly among treatments (Table 3c, Fig. 4d). The NMDS plot suggests the treatments form three clusters, with LC and LM, and C and AS forming two clusters of largely overlapping clouds, while FC forms its own cluster. As in the previous analyses, PERMANOVA results largely conform with the NMDS plots. For hydrophilids, the greatest similarity among replicates, within treatments, again occurred in the AS patches (71.93), while the lowest similarity again occurred among the LM patches (44.40). AS and C treatments were the most similar (64.45) and not significantly different, while LC and AS showed the greatest dissimilarity (34.53). All three avoided fish treatments were significantly different from both the Controls and AS, but only LC and FC were significantly different among the avoided fish (Table 3c, Fig. 4d). Separation of FC from C and AS is largely driven by the impact of *Paracymus*, whose responses track more closely with dytiscids than other hydrophilids. Separation of FC from LC and LM is driven by remaining hydrophilids, which do not avoid FC. Removal of *Paracymus* from the analysis for hydrophilids pushed the FC cluster into considerable overlap with C and AS (Table 3d, not shown).

If we examine dissimilarity as an indicator of beta diversity, the avoided fish treatments (FC, LC, LM) as a

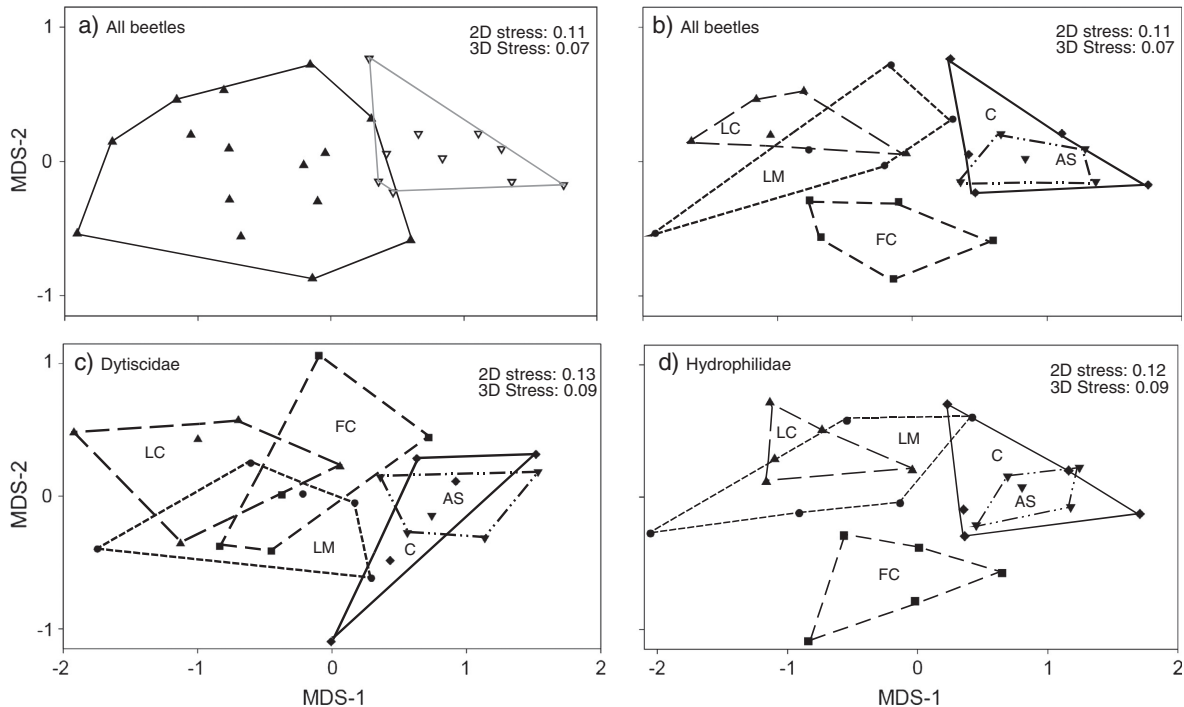


FIG. 4. NMDS minimum polygon plots of (a) avoided fish (FC, LC, LM) vs. control + AS treatments, (b) all treatments for all beetles combined, (c) all treatments for Dytiscids, and (d) all treatments for Hydrophilids.

whole generate higher beta diversity (average similarity 56.19) than the combined control and AS treatments (65.52). Some component of this is a result of lower abundance generating greater differences via stochastic processes, as the treatments fall out in different positions along the species/abundance curve (Fig. 2a). However, the effect of fish on beta diversity in aquatic beetles also generates differences after correction for abundance (A. C. Stier and W. J. Resetarits, *unpublished manuscript*). If we examine presence-absence similarity, using either Bray-Curtis or Jaccard, combined control and AS treatments vs. avoided treatments were significantly different ($P = 0.029, 0.039$ respectively). If we look at all treatments, only LC stands out as significantly different from the non-avoided treatments (C, $P = 0.034, 0.05$; AS, $P = 0.033, 0.033$) and is marginally different from FC ($P = 0.079, 0.081$). Thus, the major impact on diversity is mediated through effects on abundance, but there remains a direct effect of fish species identity on the assemblage of colonizers.

DISCUSSION

It is increasingly apparent that fish are a dominant driver not only of post-colonization sorting in freshwater systems, but of colonization dynamics themselves (Wellborn et al. 1996, Binckley and Resetarits 2009, Chase et al. 2009, Kraus and Vonesh 2010, Resetarits and Silberbush 2016). While most larger, permanent ponds contain multiple fish species, smaller ponds and those at

the temporary-permanent boundary often contain limited assemblages or even single species, depending on colonizing abilities, hardiness, and stochastic natural events (Trexler et al. 2001, Pearl et al. 2005, Petranka and Holbrook 2006). Equally relevant is that, in our increasingly human-dominated landscape, previously fishless habitats are often “stocked” with fish, including single-species introductions, for a variety of purposes. Well-known examples include the stocking of *Gambusia* and other species into previously fishless habitats worldwide for mosquito control, and widespread stocking of trout (and other species, including *L. cyanellus*) into previous fishless habitats in the western United States. Many of these fish readily establish and often expand to nearby habitats. Thus, it is relevant to consider how colonizers respond to the specific identity of potential fish invaders, whether natural or anthropogenic, since long-established ponds with diverse fish assemblages are unlikely habitats for species that typically colonize small, fishless, permanent to semi-permanent ponds. This dramatic, state-change event, going from fishless to fish (which has analogies in other systems), puts a premium on adaptive colonization/oviposition decisions in real time, and creates the greatest potential for generating ecological traps or population sinks in the absence of adaptive decision making (Schlaepfer et al. 2002, Kristan 2003). An important question is whether colonizers perceive and respond to this fishless-fish dichotomy, or perceive and respond to the more complex landscape of actual predation risk.

TABLE 3. PERMANOVA results.

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)	Unique perms	LC	AS	FC	C	LM
(a) All beetles											
Block	4	6,681.6	1,670.4	2.68	0.001	998					
Fish species	4	11,760	2,940	4.72	0.001	999					
Residuals	16	9,968.4	623.0								
Total	24	28,410									
Similarity between/ within Fish species											
LC							61.97				
AS							41.89	71.93			
FC							53.92	51.87	58.65		
C							42.48	66.00	50.54	57.87	
LM							57.03	49.44	55.79	49.05	52.51
(b) Dytiscids											
Block	4	5,596.1	1,399	3.00	0.001	998					
Fish species	4	8,174.1	2,043.5	4.38	0.001	999					
Residuals	16	7,470.3	466.9								
Total	24	21,240									
Similarity between/ within Fish species											
LC							66.31				
AS							49.56	72.63			
FC							61.31	59.09	63.35		
C							49.25	68.72	58.10	62.91	
LM							61.44	58.82	65.41	56.93	61.64
(c) All Hydrophilids											
Block	4	7,215.6	1,803.9	2.20	0.009	999					
Fish species	4	15,913	3,978.2	4.85	0.001	997					
Residuals	16	13,126	820.4								
Total	24	36,254									
Similarity between/ within Fish species											
LC							60.49				
AS							34.53	71.93			
FC							45.23	47.22	55.16		
C							36.80	64.45	45.48	54.80	
LM							54.79	40.41	47.42	42.01	44.40
(d) Hydrophilids, no <i>Paracymus</i>											
Block	4	12,640	3,160	1.82	0.022	999					
Fish species	4	15,176	3,794.1	2.19	0.017	999					
Residuals	16	27,768	1,735.5								
Total	24	55,584									
Similarity between/ within Fish species											
LC							37.84				
AS							27.12	61.93			
FC							22.34	52.61	46.23		
C							27.52	52.49	45.95	40.25	
LM							31.21	29.22	29.11	28.13	16.88

Note: Boldface type indicates significantly different factors or treatments ($P < 0.05$).

Treefrogs have been quite uniform in their responses to fish with dramatically different predatory capabilities, suggesting functional equivalence in habitat selection responses (e.g., Binckley and Resetarits 2003, Resetarits and Binckley 2013). This is consistent with the hypothesis

of a generalized fish kairomone as the cue. Here we begin to see interesting variation in community metrics that suggest a more complex dynamic. As observed previously (Resetarits and Binckley 2013), there is no response of beetles to the presence of pirate perch. In this experiment,

abundance, species richness, and assemblage composition are essentially identical to the controls. We have also examined beetle responses to much higher densities of AS, and seen no difference (W. J. Resetarits, *unpublished data*). This first example of generalized chemical camouflage has now been experimentally verified in three geographic areas (Virginia, Missouri, and Mississippi, USA) for three unrelated taxonomic groups (hylid treefrogs, dytiscid and hydrophilid beetles, and *Culex* mosquitoes; A. Silberbush and W. J. Resetarits, *unpublished manuscript*, Resetarits and Binckley 2013). For the avoided fish species in our experiment there are differences in species richness, but what stands out is the overall lack of response by colonizing hydrophilids (with *Paracymus* excluded) to FC, while *Paracymus* and the dytiscids responded equally strongly to FC and the other typically avoided fish. This stands in marked contrast to *Culex restuans*, which avoids FC the most strongly among 30 fish species tested (W. J. Resetarits, *unpublished data*). Interestingly, *Paracymus* groups with dytiscids along other axes of habitat selection as well (M. R. Pintar and W. J. Resetarits, *unpublished manuscript*). This constitutes the first evidence of variation in colonization or oviposition responses to different fish species (except pirate perch) by taxa other than mosquitoes, and is not related to fish biomass (Fig. 2c). Fish mass per pool varied by a factor of four (2–8 g/100 L), but all beetles (shown), non-*Paracymus* hydrophilids, dytiscids, and *Paracymus* (not shown) all show no effect of total fish biomass/pool either among or within species (Fig. 2c). This supports previous work suggesting a threshold effect of chemical cues on colonization/oviposition, with avoidance triggered by as little as 0.53 g of live fish/100 L for treefrogs (Rieger et al. 2004), and 0.82 g/100 L for beetles (Binckley and Resetarits 2005, 2009) and supports the idea that there is little, if any, dose response with respect to the operative chemical cue(s) once they pass that detection/avoidance threshold.

Our experiment shows, however, that there is interspecific variation in beetle responses driven by variation in identity or concentration of fish chemical cues, differential sensitivity to those cues, or behavioral response algorithms (beetles detect variation in cues the same way but respond differently), and that variation results in differences in species abundance and assemblage composition. Our work on pirate perch chemical camouflage suggests the absence of a recognizable cue (W. J. Resetarits, *unpublished data*), but the question of a general fish chemical cue vs. the possibility of species-specific cues remains unresolved (Resetarits and Binckley 2013).

The eight most abundant beetle species showed a variety of patterns (Fig. 3). For seven of the eight species, the AS treatment was not significantly different from Controls, and for the eighth, *U. granarius*, AS was significantly higher than Controls. Only the hydrophilid *E. ochraceus* failed to respond to any fish species, though it was the least abundant of the eight, with correspondingly lower power to detect differences. The dytiscids

Copelatus glyphicus, *U. granarius*, and *H. niger*, along with the hydrophilid *Paracymus*, showed the typical pattern of avoidance of all fish except AS, while the hydrophilid *T. lateralis* only avoided the *Lepomis* species, reflecting the overall hydrophilid response. The two *Laccophilus* species avoided both *Lepomis*, but had somewhat, though but not significantly, reduced numbers with FC.

Why would dytiscid and hydrophilids respond differently to specific fish predators? Unlike treefrogs or mosquitoes, adult beetles choose a habitat both for themselves and their offspring. Adults are obligately aquatic, as are larvae (except for *Helophorus*), which then pupate on land at the pond margin. Larvae of dytiscid and hydrophilid beetles are morphologically and ecologically similar: both are voracious predators known collectively as “water tigers.” The major ecological difference is the feeding habits of adults, with dytiscids being carnivorous, like their larvae, while adult hydrophilids, known as water scavenger beetles, are omnivorous. Are the decisions of hydrophilids driven more by adult survival and performance than survival/performance of their offspring? It is interesting to note that the smallest of our beetles, *Paracymus*, very strongly avoided FC, which is a small, gape-limited predator, while the larger hydrophilids, such as species of *Tropisternus*, did not. A similar pattern occurs in the small helophorid *Helophorus linearis* (w/terrestrial larvae), and the very small hydrophilid *Berosus exiguus*. Intermediate-size hydrophilids, such as most *Berosus* and *Enochrus*, showed somewhat reduced avoidance of FC, though numbers for individual species were too low for meaningful analysis, except for *E. ochraceus* (Fig. 3). However, ANOVA on abundance for hydrophilids categorized as “large” vs. “small” (leaving out intermediate species and *Paracymus*) indicated no avoidance of FC in either group. Parsing the data in this manner reduced overall numbers, so the results are not definitive. Dytiscid and hydrophilid larvae are affected by fish as both predators and competitors, while fish may affect hydrophilid adults only as potential predators, and dytiscid adults as both predator and competitor. More work is required to sort out this interesting difference in responses.

Predators may affect prey via both lethal and non-lethal effects on distribution and abundance, and these two types of processes may interact to determine species composition and community structure. Different predators, in this case different species of fish, may have characteristic lethal effects on a suite of prey species because of variation in predatory capacities that then lead to a species-specific local extinction rate. However, also because of different predator traits, these local extinction rates differentially affect subsets of prey that vary in vulnerability to specific predators.

Predators may also have characteristic non-lethal effects on species distribution and abundance expressed via habitat selection behavior, and the non-lethal effects of different fish are not necessarily predictable from

lethal effects. This is certainly true with AS, which has no non-lethal effects on immigration (W. J. Resetarits, *unpublished data*, Resetarits and Binckley 2013), but strong lethal effects (Albecker and Vance-Chalcraft 2015; W. J. Resetarits, *unpublished data*). This contrasts with gape-limited fish like the golden topminnow, *Fundulus chrysotus*, or golden shiners, *Notemigonus crysoleucas*, whose predatory impacts are rather limited, but produce significantly lowered immigration rates (FC this study) or truly dramatic reductions equivalent to the most voracious predators (*N. crysoleucas*; W. J. Resetarits, *unpublished data*). In between, species like *Lepomis cyanellus*, and in the extreme, species of *Esox*, have lethal and non-lethal effects that are both very strong.

The problem of integrating the combined effects of lethal and non-lethal processes to understand the impact of predators on natural communities is certainly not unique to freshwater systems, but is relevant to any system potentially containing a variety of predators, especially those where predator avoidance behaviors (non-lethal effects) are mediated via environmental cues that serve as indicators of predator location. Africa's large predator guild contains five species (lion, leopard, spotted hyena, cheetah, and African wild dog) that are broadly sympatric and utilize a similar range of prey (Hayward and Slotow 2009). However, the non-lethal impacts of the differing predator species varies based on both the identity of the predator and identity of the prey; smaller prey species avoided areas containing all five large predators, whereas larger species only avoided areas with evidence of lions and leopards (Thaker et al. 2011). Thus, all five predator species are functionally equivalent in their non-lethal effects on smaller prey, but divide into two distinct groups with respect to larger prey. In this case, lethal and non-lethal effects may match fairly well, that is, non-lethal effects are broadly predictable from the magnitude of lethal effects, though this likely varies as well. Here too, chemical cues of the five predators could be expected to be uniquely identifiable by the prey. In a marine system off the coast of South Africa, 13 species of large sharks are highly functionally diverse in their lethal effects, but the non-lethal effects—how species respond to this diverse, but closely related, group of predators—is unknown (Hussey et al. 2015). Species-specific cues may be less tractable among such closely related species, so prey may respond to a generalized “shark” cue resulting in mismatched lethal and non-lethal effects. In our system, we have seen such distinct mismatches between lethal and non-lethal effects, which then generate greater potential variation in predator-specific impacts across a complex landscape of habitat patches (Resetarits and Binckley 2013; this study). In our system, the number of potential local predator species, just considering fish, is at least an order of magnitude higher than in the African carnivore system (Mississippi contains 280 species of freshwater fish), limiting the likelihood of species-specific identity cues (Resetarits and Binckley 2013).

Lethal and non-lethal effects of predators obviously have important consequences for communities, but these are manifested via impacts on individual species. There are potentially significant consequences of both over- and underreacting to the severity of lethal effects. Underreacting puts colonists or offspring into high-risk situations, while overreacting can result in missed opportunities resulting from avoidance of low-risk habitats.

Non-lethal impacts on immigration rates can be as important as lethal effects in determining species distributions and community structure, and, because effects on the immigration side of the equation precede any lethal effects, they may also obviate them if sufficiently strong. Non-lethal effects may also vary in their relationship to the magnitude of lethal effects. How different species of predators affect community structure and resultant properties, like ecosystem function, can vary as a result of both lethal and non-lethal effects, as well as their interaction. Because those effects can vary independently, or are often mismatched, the variety of effects produced by predators is enhanced and the prospects for functional equivalence/redundancy within any suite of predators is reduced. Add to that the fact that prey taxa react differently to different predators, and the prospects for functional equivalence of effects is rather remote, even within phylogenetically related species (Loreau 2004, Resetarits and Chalcraft 2007, Losos 2008). For ovipositing treefrogs (Binckley and Resetarits 2003, Resetarits and Binckley 2013) and colonizing dytiscid beetles (this study), a fish may be a fish (with the exception of *A. sayanus*), but not for colonizing hydrophilids (this study) or ovipositing mosquitoes (W. J. Resetarits, *unpublished data*, Vonesh and Blaustein 2011, Eveland et al. 2016). Thus, variation among taxa in non-lethal responses further enhances a complex landscape of predator effects in freshwater systems that defies simplistic notions of functional redundancy.

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