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Colonization across gradients of risk and reward: Nutrients and predators generate species-specific responses among aquatic insects

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Abstract

1. Predation risk and resource abundance are two primary characteristics that determine species abundances and community composition. Colonizing organisms should attempt to minimize the risk of mortality and maximize growth through selection of patches with the highest expected fitness. However, maximizing fitness across multiple gradients of patch quality involves accurate cue assessment, integration and behavioural responses that consider multiple factors that affect fitness simultaneously.
2. Our goal was to simultaneously and factorially assess the effects of predation risk and resource abundance among an assemblage of aquatic insects to determine the relative importance of each factor, and whether the two factors interact to affect colonization, oviposition and community assembly.
3. We conducted a field mesocosm experiment in which we crossed predator density (0, 1, 2 fish, *Fundulus chrysotus*) with supplemental nutrient abundance (0, 4, 8 g rabbit chow) in a 3 × 3 factorial design. We then assayed colonization by natural populations of aquatic beetles and oviposition by natural populations of *Culex* mosquitoes.
4. We observed species-specific responses, with many species avoiding fish and some selecting habitats with more nutrients. Nutrients and predator presence only interactively affected oviposition by *Culex* mosquitoes, and the effect of fish presence exceeded that of nutrients in all but one analysis.
5. Our results illustrate the primacy of predation risk in generating colonization patterns and structuring communities in aquatic habitats, but that colonization responses to variation in multiple components of patch quality are often species-specific. Simultaneous assessments of multiple aspects of patch quality allow for the determination of potential interactions among cue sources and the relative importance of various patch characteristics to colonizers.

KEYWORDS
colonization, community assembly, *Culex*, Dytiscidae, habitat selection, Hydrophilidae, oviposition, predation risk

1 | INTRODUCTION

Determining the mechanisms generating spatial variation in species abundance is critical to understanding patterns of biodiversity across landscapes (Chesson, 2000; MacArthur & Wilson, 1967). Lethal effects have been traditionally viewed as the dominant drivers of species distributions and community structure, but nonlethal processes can have effects that rival or exceed those of lethal effects (Cresswell, 2008; Heithaus, Wirsing, Thomson, & Burkholder, 2008; McCauley, Rowe, & Fortin, 2011; Resetarits & Binckley, 2009; Rieger, Binckley, & Resetarits, 2004; Vonesh, Kraus, Rosenberg, & Chase, 2009). In particular, potentially lethal effects can be reduced or avoided via habitat selection, a process where dispersing organisms assess habitat characteristics based on the perceived quality (expected fitness) of a patch. Habitat quality can be defined by various factors, but ultimately integrates variation in risk and reward (Moody, Houston, & McNamara, 1996; Nonacs & Dill, 1990). In aquatic systems, the presence and identity of predators (Wellborn, Skelly, & Werner, 1996) and productivity are major determinants of patch quality (Fukami & Morin, 2003). Patches with predators are typically higher risk, whereas patches with high productivity are typically higher reward. Trade-offs between risk and reward impact behaviour, influencing evolutionary pathways and ultimately determining patterns of species coexistence (McPeek, 2004).

Balancing predation risk and resource acquisition is the most fundamental trade-off faced by many organisms (Charnov, 1976; Holbrook & Schmitt, 1988; Houston, McNamara, & Hutchinson, 1993; Sih, 1980). Riskier behaviour in the face of predation is associated with increased mortality, but can also result in greater reward (Brown, 1988; Brown, Laundre, & Gurung, 1999; Pitcher, Lang, & Turner, 1988; Werner & Hall, 1988). Thus, minimizing the ratio of mortality (μ) to growth rate (g) has become a dominant paradigm in ecology (Werner & Gilliam, 1984) and has recently been applied to colonization behaviour (Binckley & Resetarits, 2008). Optimal habitats, presumably assessed based on risk and reward, are often colonized first, maximizing expected fitness (Fretwell & Lucas, 1970; Rosenzweig, 1991).

Colonizing organisms rely upon environmental cues that indicate habitat quality and depend upon accurate assessment and response to variation in patch quality in order to maximize fitness in complex landscapes (Blaustein, Kiflawi, Eitam, Mangel, & Cohen, 2004; Ferrari, Wisenden, & Chivers, 2010). When multiple cues representing variation in multiple indicators of habitat quality are presented simultaneously, organisms must evaluate and choose between patches along such simultaneous gradients. Often these multiple gradients consist of variation in indicators of relative risk and reward. Accuracy of cue assessment may diminish if organisms cannot properly interpret trade-offs associated with cue mixtures (Peacor, 2006; Strom, Goyer, & Shea, 2001), are presented with novel cues or novel cue mixtures, cannot detect or identify multiple cues simultaneously (Hankison & Morris, 2003), or cues are presented outside of the temporal, spatial or behavioural context in which they evolved (Burley & Symanski, 1998). Determining the relative importance of risk, reward and their potential interactions is critical to interpreting observed patterns of colonization and community assembly.

Colonization and oviposition by adult aquatic insects is a useful system for examining habitat selection dynamics, as they utilize habitat patches (ponds) that are easily mimicked using artificial mesocosms. They select habitat patches based on both predation risks (Layton & Voshell, 1991; Resetarits & Binckley, 2009; Resetarits & Pintar, 2016; Silberbush & Blaustein, 2011), which affect both themselves and their offspring, and resource levels, which impact adult reproductive output and larval growth (Pintar & Resetarits, 2017c; Reiskind & Wilson, 2004; Tatar & Carey, 1995). During the colonization process, insects use several sensory modalities to find patches and assess quality at multiple spatial scales, with assessment of chemical cues, and kairomones in particular, playing a prominent role (Bilton, 2014; Bilton, Freeland, & Okamura, 2001; Eveland, Bohenek, Silberbush, & Resetarits, 2016; Resetarits & Binckley, 2013). Initial colonization decisions are critical, whether or not individuals secondarily disperse, as dispersal via flight is energetically costly, and once settlement is complete secondary dispersal may occur only if conditions dramatically change (Bilton, 2014; Layton & Voshell, 1991; Zalom, Grigarick, & Way, 1979). Some species autolyse flight muscles and reallocate resources to reproduction or swimming muscles after colonization (Johnson, 1969; Zera & Denno, 1997).

We assayed colonization by natural populations of dispersing adult beetles and oviposition by *Culex* mosquitoes in response to variation in predation risk and nutrient levels. Predators, and fish in particular, play critical roles in structuring communities in freshwater systems through both their lethal effects (predation) and their nonlethal effects on habitat selection behaviours of colonizing prey (Binckley & Resetarits, 2005; Carpenter, Kitchell, & Hodgson, 1985; Power, 1990; Wellborn et al., 1996). Many colonizing beetles and ovipositing *Culex* respond positively to increased resource levels that drive higher primary and secondary productivity (Pintar & Resetarits, 2017a; Reiskind & Wilson, 2004), including higher prey abundances for predaceous beetles (Leibold, 1999). Known responses of colonizing beetles and ovipositing *Culex* to variation in nutrient levels and predator presence served as the basis for our predictions (Table 1). However, in most of these prior studies, nutrients and fish were studied independently; there is a lack of factorial assessments in which both were manipulated simultaneously (but see Binckley & Resetarits, 2008). Responses to both nutrients and fish are often taxon-specific, but for many species colonizing aquatic habitats, fish presence/absence would be expected to be the primary driver of perceived patch quality (Resetarits & Binckley, 2014; Rieger et al., 2004). We hypothesized that under an adaptive decision-making framework colonists would avoid patches with higher fish density, prefer patches with greater resources, and if the two interacted, display a trade-off between predation risk and resource levels by colonizing patches of greater predation risk only when resource levels were high. Additionally, we predicted the magnitude of the effect of predators would be greater than that of nutrient addition due to the immediacy of the risk of death associated with predator presence (Binckley & Resetarits, 2008).

TABLE 1 Known responses of taxa in our experiment to variation in patch nutrient availability, fish presence (generalized across multiple fish species) and *Fundulus chrysotus* presence

Taxa	Nutrients	Fish (generalized)	*Fundulus chrysotus*
Beetles (all)	Y[a]	Y[b,c,d]	Y[b]
Dytiscidae	Y[a]	Y[b,c,d]	Y[b]
Hydrophilidae	Y[a]	Y[b,c,d]	N[b]
Copelatus glyphicus	Y[a]	Y[b,c,d]	Y[b]
Cymbiodyta chamberlaini	?	N[d]	?
Enochrus ochraceus	Y[a]	Y[b,c,d]	N[b]
Laccophilus fasciatus	Y[a]	Y[b,c,d]	N[b]
Paracymus	Y[a]	Y[b,d]	Y[b]
Culex	Y[e]	Y[f,g]	Y[f]

Y indicates that taxa are selective for variation in that characteristic across patches—higher colonization with more nutrients, lower colonization with fish presence. N indicates no selection shown; ? indicates an unknown response.

[a] Pintar and Resetarits (2017b).

[b] Resetarits and Pintar (2016).

[c] Resetarits and Binckley (2014).

[d] W. J. Resetarits, M. R. Pintar, J. R. Bohenek, and T. M. Breech (unpublished data).

[e] Reiskind and Wilson (2004).

[f] J. R. Bohenek, M. R. Pintar, L. L. Eveland, T. M. Breech, and W. J. Resetarits (unpublished data).

[g] Bohenek, Pintar, Breech, and Resetarits (2017).

2 | MATERIALS AND METHODS

We conducted a field mesocosm experiment from May to June 2015 at the University of Mississippi Field Station (UMFS) using plastic wading pools (0.85 m diameter, 70 L) as experimental ponds. Pools (pool = habitat patch) were filled with unchlorinated well water and had 0.5 kg of dry, predominantly hardwood leaf litter (primarily *Quercus* spp.) added as a nutrient base. Many small ponds, particularly those in forested ecosystems, receive the bulk of their nutrients via such allochthonous inputs, which drive primary and secondary productivity in most freshwater systems (Minshall, 1967). We covered pools with fibreglass screening (1.3 × 1.13 mm opening) that was depressed below the water surface to separate beetles/*Culex* eggs from the leaf litter and prevent direct physical interaction between insects and predators (located below the screens), while still allowing insects to detect fish kairomones and colonize pools. Treatments were randomly assigned to pools within each block and consisted of a complete 3 × 3 factorial design with three densities of predators (0, 1, 2 fish per 70-L pool) crossed with three levels of supplemental nutrient addition (0, 4, 8 g rabbit chow: Small World Rabbit Food, Mannapro, St. Louis, MO, 40% protein). Rabbit chow is a nutrient-dense resource commonly used in manipulations of nutrient levels/productivity (Binckley & Resetarits, 2008; Blaustein & Kotler, 1993; Relyea, 2002; Semlitsch & Boone, 2010).

We set up nine blocks of nine pools arranged parallel to a tree line (original $N = 81$), with pools separated by 5 m edge-to-edge in three fields (location factor) at UMFS. Relatively large interpatch distances (5 m) among our patches were used to eliminate the possibility of spatially context-dependent processes among patches, such as contagion (Resetarits, Binckley, & Chalcraft, 2005). Blocks were located ~25 m from nearby water bodies that served as potential sources of colonists, although all of the 200+ local ponds at UMFS may serve as potential colonist sources. Each block was run for 14 days (time factor): three blocks from 13 May to 27 May, three from 27 May to 10 June and three from 11 June to 25 June. The short temporal duration of each block was sufficient to assay colonization of several beetle species and oviposition by *Culex* mosquitoes. Blocking by location was necessary due to space limitations, whereas blocking by time was necessary to ensure adequate replication.

The fish species used was the golden topminnow, *Fundulus chrysotus* (Fundulidae), a small fish (average mass 1.14 g) known to elicit colonization avoidance behaviours via chemical cues among Dytiscidae and ovipositing *Culex restuans*, but not some Hydrophilidae (Resetarits & Pintar, 2016; J. R. Bohenek, M. R. Pintar, L. L. Eveland, T. M. Breech, & W. J. Resetarits, unpublished data). We used low numbers (one, two) of fish per patch to allow us to investigate per capita effects and due to the small volume of our mesocosms and the propensity for intraspecific aggression in *Fundulus* (Carranza & Winn, 1954). *Fundulus chrysotus* are surface-feeding predators common in ponds at UMFS, there are no reports of them feeding on vegetable matter, and we did not provide them with supplemental food. Resting stages of zooplankton introduced with leaf litter and passive colonization by both zooplankton and eggs and/or offspring of insects that sink through the screens provide sufficient food for fish in our mesocosms.

Because we were interested in primary habitat selection behaviours and not changes with community assembly over time, beetles were exhaustively collected without replacement halfway through (7 days) and at the termination (14 days) of each block. Beetles from both sampling dates within temporal/spatial blocks were summed to obtain cumulative patch totals, which were used in analyses. All beetles were preserved in ethanol and identified to species, with the exception of the genus *Paracymus*, which were only identified to genus (95% of those previously identified from

UMFS are *P. subcupreus*). Beetle species identifications were conducted primarily using Testa and Lago (1994), Larson, Alarie, and Roughley (2000) and Epler (2010). Mosquito egg rafts were counted each morning and removed from pools. A total of 47 egg rafts from the first five blocks were reared to fourth instar and identified to species (Darsie & Ward, 2005). All individuals were identified as *C. restuans*, which concurs with previous work that found ~99% of the thousands of identified *Culex* egg rafts at UMFS were *C. restuans* (J. R. Bohenek unpublished data).

The screens created a visual barrier in the pools, so we were unable to monitor fish mortality during the experiment. Fish were collected and massed when each block was terminated, and there were a total of 12 pools with 15 missing or dead fish. We excluded all pools that experienced fish mortality, resulting in a total of 69 mesocosms included in our analyses (Table 2). Half of pools with fish mortality belonged to the two fish/8-g treatment, with relatively even distribution of mortality among the other treatments containing fish. Seven of the twelve pools with mortality were in time 3/location 3 (blocks 7, 8 and 9). Our response variables were the mean abundance of all beetles per patch, Dytiscidae, Hydrophilidae, and species with abundances >50, as well as beetle species richness. We also analysed the mean number of *Culex* egg rafts per night in each pool.

We examined the effect of predator density (number of fish per patch), nutrient addition (0, 4, 8 g rabbit chow) and the nutrient × predator density interaction on each of our response variables in factorial linear-mixed effects models (Satterthwaite Type III SS; Kuznetsova, Brockhoff, & Christensen, 2017) that included blocking factors (location and time) as random effects. The analysis of beetle species richness included overall beetle abundance as a covariate to determine whether richness varied independently of abundance. We used PERMANOVA to assess the effects of nutrients and predators on beetle assemblage structure; PERMANOVA again included time and location as random effects and nutrients and predator density as fixed effects. The nutrient × predator density interaction was not significant for most analyses ($p > .25$) and was rolled into the error term; this interaction was maintained in analyses when $p < .25$. Count data were square-root transformed ($\sqrt{X+0.5}$). Analyses used $\alpha = 0.05$ and were conducted using R v 3.4.1 (R Core Team, 2017), LME4 package v 1.1-13 for mixed models (Bates, Mächler, Bolker, & Walker, 2015), and PRIMER v 7.0.13 and the PERMANOVA+ add-on for PERMANOVA analyses and to generate the NMDS plot (Anderson, Gorley, & Clarke, 2015; Clarke & Gorley, 2015).

TABLE 2 Number of replicates for each treatment of predator density (0, 1, 2 fish per pool) crossed with added nutrients (0, 4, 8 g of rabbit chow)

	Predator density		
Nutrients	**0**	**1**	**2**
0	9	9	8
4	9	7	8
8	9	7	3

This table is the final number of replicates used in analyses and excludes all pools with missing or dead fish. The original number of replicates for each pairwise combination was nine.

3 | RESULTS

Excluding patches with fish mortality, our experiment was colonized by 1,673 individual beetles of 23 species in four families; five beetle species were abundant enough for individual analysis (Table 3). Mosquitoes laid 634 egg rafts over the course of our experiment, excluding patches with fish mortality. We observed main effects of fish presence in most analyses, with higher colonization of fishless patches than patches containing either one or two fish, whereas nutrients had a positive effect on colonization for several species, with higher colonization of patches with more nutrients (Figure 1; see Appendix S1). Among all beetles, fishless patches had highest colonization, and patches with 8 g of added nutrients were colonized at higher rates than patches with 0 or 4 g of added nutrients (Figure 1a), but there were no interactions between nutrients and fish; this is the same pattern that we observed for dytiscids (Figure 1b). Hydrophilids (Figure 1c) had lower colonization of patches containing fish and a marginal effect of nutrients, but no interaction between nutrients and fish. Species richness (Figure 1d) was unaffected by fish or nutrients, but covaried with beetle abundance; richness was higher when overall beetle abundance was higher (Figure 2). *Copelatus glyphicus* (Figure 1e), the most common beetle and dytiscid, colonized fishless patches and those with more nutrients at higher rates. *Cymbiodyta chamberlaini* (Figure 1f), the most common hydrophilid, selected patches with higher amount of nutrients, but colonized fish and fishless patches at equal rates. Colonization by *Enochrus ochraceus* (Figure 1g) was highest in fishless patches, but was unaffected by nutrients. *Laccophilus fasciatus* (Figure 1h) were low in abundance, but their colonization rates had a marginal effect of fish and no effect of nutrients and no interaction.

TABLE 3 Species and abundances of colonizing beetles

Dytiscidae	1176	Helophoridae	3
Acilius mediatus	2	*Helophorus linearis*	3
Copelatus chevrolati	15		
Copelatus glyphicus	1066	Hydrophilidae	493
Hydaticus bimarginatus	5	*Berosus exiguus*	4
Hydrocolus deflatus	5	*Berosus infuscatus*	8
Hydrocolus oblitus	9	*Cymbiodyta chamberlaini*	226
Laccophilus fasciatus	59	*Cymbiodyta vindicata*	1
Laccophilus proximus	6	*Enochrus consortus*	1
Mediorhantus calidus	1	*Enochrus ochraceus*	128
Neoporus blanchardi	2	*Enochrus perplexus*	15
Platambus flavovittatus	1	*Paracymus*	76
Uvarus granarius	5	*Tropisternus lateralis*	34
Haliplidae	1		
Peltodytes muticus	1		

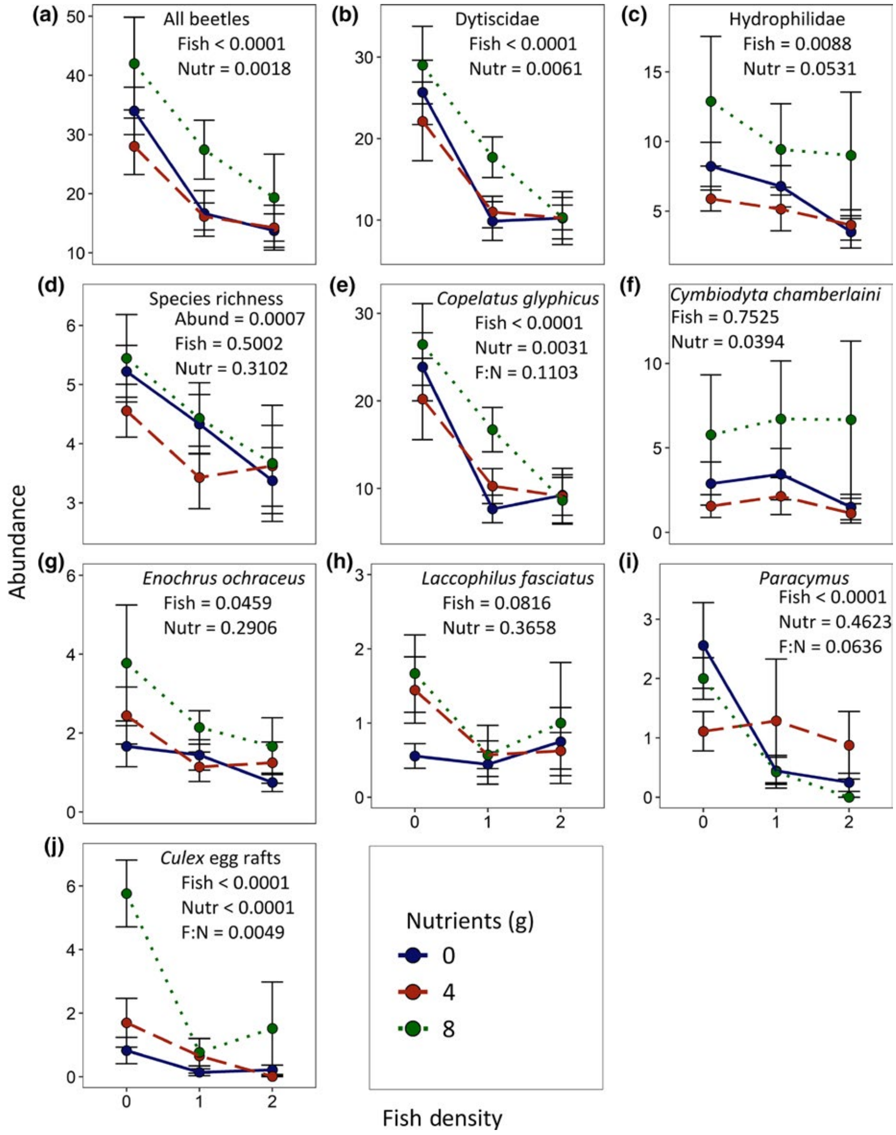

FIGURE 1 Mean abundances of colonists per patch (± *SE*) across a gradient of predator density (number of fish per patch; x axis) and grouped by amount of supplemental nutrients. Each point represents the mean for one of the nine treatments in the 3 × 3 factorial design. *p* values from analyses are listed for the effects of fish (Fish), nutrients (Nutr) and the fish × nutrient interaction (F:N; when included, see Section 2 and Appendix S1), and beetle abundance (Abund) when included as a covariate. *Culex* egg rafts (j) are nightly means per patch

Paracymus (Figure 1i) also colonized fishless patches at higher rates with a marginal interaction and were unaffected by nutrients.

Only *Culex* egg rafts (Figure 1j) had a significant fish × nutrient interaction. There were more *Culex* egg rafts in fishless patches and patches with added nutrients, and the interaction could be due to a steeper response to the presence of predators in patches with 8 g of added nutrients (Figure 1j). As shown with PERMANOVA, beetle assemblage structure varied with fish density ($F_{2,60}$ = 3.76; *p* = .001; Figure 3a) but not nutrients ($F_{2,60}$ = 1.28; *p* = .244; Figure 3b); fishless patches had distinct assemblages from fish patches. There was no fish × nutrient interaction, but there were significant effects of location ($F_{2,60}$ = 4.54; *p* = .001; Figure 3c) and time ($F_{2,60}$ = 7.11; *p* = .001; Figure 3d) on beetle assemblage structure.

4 | DISCUSSION

Our data demonstrate that two components of patch quality in aquatic systems, predator presence and nutrient abundance, influence the colonization rate of aquatic beetles and oviposition by *Culex* mosquitoes. The species colonization patterns we observed (Figure 1) largely matched our predictions based on independent manipulations of these two factors (Table 1). We expected a strong primacy of predation risk over reward; predation risk typically outweighs the effects of other factors due to the immediacy/finality of the risk of death, and effects of more predators have threshold (presence/absence), not additive, effects on colonization (Brown & Kotler, 2004; Holbrook & Schmitt, 1988; Thompson, 2013). In other studies of risk/reward gradients, predation risk typically has consistently strong effects that outweigh reward (Binckley & Resetarits, 2008; Blaustein & Kotler, 1993; Reiskind & Wilson, 2004). In our study, fish presence regardless of density was the dominant driver of colonization for all species, except *Cymbiodyta chamberlaini*, and nutrients and predator presence did not interact, except among ovipositing *Culex*; colonization responses to both nutrients and predation risk are largely independent and clearly species-specific.

Our five common beetle species and *Culex* larvae form a group of animals with diverse trophic roles, morphologies and life histories,

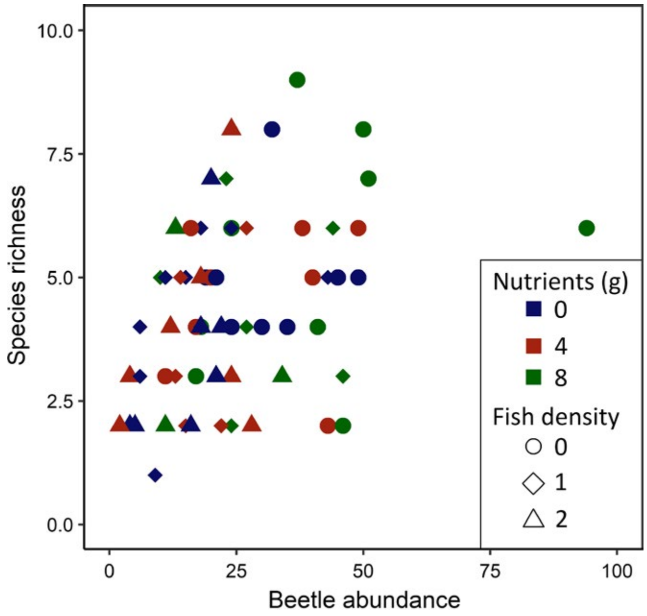

FIGURE 2 Species abundance curve illustrating beetle species richness vs. overall beetle abundance in each pool

which might partially explain the observed colonization patterns. *Copelatus glyphicus* and *Laccophilus fasciatus* are small dytiscids (predaceous diving beetles), whereas *Cymbiodyta chamberlaini*, *Enochrus ochraceus* and *Paracymus* are small hydrophilids (omnivorous scavengers). *Laccophilus fasciatus* is a highly competent swimmer with a robust body, both of which may help it avoid predation by the relatively small *F. chrysotus* and explain why only nonsignificant, but marginal, effects have been observed on its colonization (Figure 1h; Resetarits & Pintar, 2016). *Copelatus glyphicus* is a competent swimmer, but has a much less robust body than *L. fasciatus* and is highly vulnerable to other predators, such as aquatic hemipterans (M. R. Pintar & W. J. Resetarits, unpublished data). *Paracymus* and *E. ochraceus* are two of the smallest hydrophilids that are often found close to the water surface, likely placing them at high risk of predation by *F. chrysotus*. *Cymbiodyta chamberlaini* is somewhat larger, with its size potentially excluding it from predation by *F. chrysotus*. However, *C. chamberlaini* also does not avoid other larger fish species (W. J. Resetarits, M. R. Pintar, J. R. Bohenek, & T. M. Breech, unpublished data), questioning whether its lack of avoidance of *F. chrysotus* is related to size (Figure 1f). *Culex* larvae are relatively soft-bodied filter feeders that live predominately at the water's surface and have short duration larval stages. These characteristics would make *Culex* particularly prone to predation by *F. chrysotus*, yet responsive to variation in nutrient levels, which would accelerate larval development (Reiskind, Walton, & Wilson 2004; A. Silberbush and W. J. Resetarits, in review).

Even though predaceous beetle species do not directly feed on the rabbit chow or leaf litter, base resources and nutrients support higher primary productivity, which in turn supports higher abundances of prey taxa (zooplankton, larval insects) as well as food for

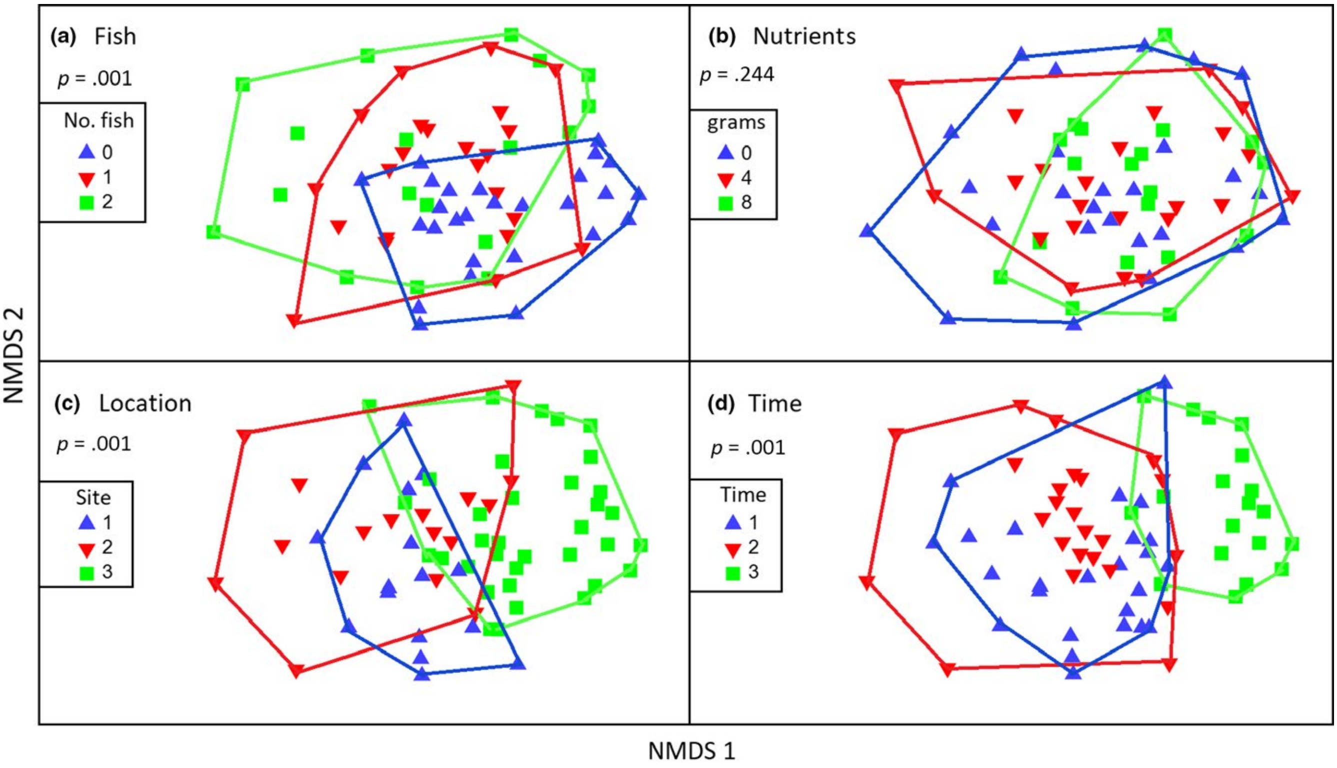

FIGURE 3 NMDS plots of beetle assemblages. Points are illustrated and enclosed minimum convex polygons based on (a) predator density (0, 1, 2 fish per pool), (b) nutrients added (0, 4, 8 g rabbit chow), (c) location (site 1, 2 or 3) and (d) time (times 1, 2 or 3; see Section 2). *p* values indicate significance of each factor in PERMANOVA. Graphs exclude one outlier (a two fish, 8 g pool). 2D stress = 0.21; 3d stress = 0.15

the omnivorous hydrophilids. The predaceous dytiscids select habitats with higher abundances of zooplankton, whereas hydrophilids do not, while both families select patches with more leaf litter (Pintar & Resetarits, 2017a, 2017b). This indicates that aquatic beetles can be responsive to both the resources they directly use and the overall nutrient availability. Given that our mesocosms were immediately opened for colonization upon filling and were only set up for 14 days, we expect that *C. glyphicus* and dytiscids overall were at least initially responding directly to rabbit chow addition and not tri-trophic interactions that would result in greater prey abundance.

Adult beetles select habitats for their offspring in addition to themselves, which contrasts with the oviposition-only decisions made by adult female *Culex*. We would expect beetle colonization preferences to be more indicative of the risk/reward that their offspring would experience in these habitats, yet this is clearly not the case. The eggs and larvae of the small beetle species that colonized our experiment would be much more vulnerable to predation by even small predatory fish, such as *F. chrysotus*, as the exoskeleton of beetle larvae is typically not as durable as that of adults. If beetles chose patches to exclusively maximize offspring performance, we would expect stronger predator avoidance among all five of our common species. It is possible that these beetles select habitats and do not breed in them due to this risk; however, *Tropisternus lateralis* egg deposition was shown to be directly proportional to adult colonization in patches with and without predatory fish (Resetarits, 2001), and fish clearly had primacy over nutrients in affecting the deposition of *T. lateralis* egg cases (Binckley & Resetarits, 2008). Differential use of habitats for foraging and breeding is unlikely, as many adult beetles, for a variety of reasons, have morphologically and temporally limited dispersal capabilities, which mean that once they colonize habitat patches they settle there and do not disperse again (Iversen, Rannap, Briggs, & Sand-Jensen, 2017; Zera & Denno, 1997). Insects are able to locate and assess patches from visual (Bilton, 2014; Bilton et al., 2001) and volatile chemical cues during flight (Eveland et al., 2016; Silberbush & Blaustein, 2008). As aquatic beetles disperse and colonize patches, they likely arrive at a preferred patch (assessed in flight), further assess that patch from the pond margins or enter the patch, and then decide to settle or find another patch. This initial process of habitat selection and settlement occurs in a single night, with movement among patches days or weeks later unlikely. The consequences of these colonization decisions can be great, as both beetles and mosquitoes are potentially devoting their entire lifetime reproductive output to a single habitat patch.

How potential colonists perceive patch quality should theoretically result in colonization rates proportional to true patch quality, and experiments examining the trade-off between resources and risk typically assume perfect knowledge of those conditions, sensu the ideal free distribution (Binckley & Resetarits, 2008; Fretwell & Lucas, 1970). However, studies have typically manipulated one aspect of patch quality without allowing for assessment of their relative importance or potential interactions. Presenting multiple cues simultaneously can potentially result in inaccurate cue assessment, but this scenario is a reality in natural habitats. Thus, it is critical to assess potential cue interactions with factorial designs. The responses of our abundant species to both *F. chrysotus* and nutrient addition largely confirmed what we had expected (Table 1). This suggests that many of the taxa that colonized our experiment were able to simultaneously assess multiple cues and interpret them within the context they were present in our mesocosms. Three species (*E. ochraceus*, *L. fasciatus* and *Paracymus*) did not respond to nutrient addition where it would be expected (Figure 1, Table 1). Whether this lack of response was due to the novelty of rabbit chow or cues that these species did not recognize as being informative is undetermined, as well as the chemical structure of the exact cues being assessed (Silberbush et al., 2010). However, while we exhaustively removed all beetles weekly, we would not necessarily expect colonization patterns to change whether community assembly was allowed to proceed, as we have been unable to elicit negative density dependence among colonizing beetles at UMFS (M. R. Pintar, unpublished data).

In natural systems, nutrient availability in freshwater habitats can vary dramatically based on many factors, including substrate, surrounding habitats, pond depth and macrophytes, and fish species and abundances present. Fish typically increase available nutrients (particularly nitrogen through excretion of ammonia) in water, but their effects can vary depending on their population size and functional roles, with studies having focused on planktivorous and piscivorous fish of interest to aquaculture or recreation (Kraft, 1993; Schindler, Knapp, & Leavitt, 2001; Vanni, Flecker, Hood, & Headworth, 2002). The effects of small, surface-dwelling fish such as *F. chrysotus* are poorly understood in the context of nutrient dynamics (Cline, East, & Threlkeld, 1994; Drenner, Smith, & Threlkeld, 1996). However, it appears that fish presence and density in our experiment did not detectably affect colonization through nutrient excretion. If *F. chrysotus* would have increased available nitrogen, we might expect differences in colonization rates between patches with one or two fish among colonizing species that selected for patches based on nutrient availability; this did not occur. The lack of a positive fish effect, if it even occurs, may be in part due to the relatively small size of our fish (1.14 g) relative to the amount of supplemental nutrients added (4- and 8-g rabbit chow) as well as the overall amount of newly submerged dead organic matter (0.5 kg leaf litter) added to each pool, both likely contributing much more newly available nutrients in the water column. Even with all this organic matter, fish presence still results in habitat avoidance by most colonizing species, with equally strong avoidance with one and two fish present, indicating that fish presence and kairomones they produce are for most taxa more important patch characteristics than nutrient availability.

Habitat selection plays an important role in determining the colonization rate and resulting community structure both within and among habitat patches for aquatic insects (Binckley & Resetarits, 2005; Vonesh et al., 2009). Both predator presence and identity, and resource abundance and quality, can cause differential colonization rates that result in aquatic beetle assemblages that vary based on these patch characteristics (Pintar & Resetarits, 2017b, 2017c; Resetarits & Pintar, 2016). While we observed species-specific colonization in response to variation in nutrients and predator presence, overall assemblage structure of colonists was driven by predator presence alone, again reflecting the primacy of predation risk in freshwater habitats.

Dispersal and colonization are key processes that connect local population dynamics across larger spatial scales and generate patterns of community and metacommunity structure (Leibold et al., 2004; Morris, 2003). Predation risk and resource abundance are important characteristics that drive colonization patterns, subsequently resulting in performance differences among colonizers and their offspring (Resetarits & Pintar, 2016; Rieger et al., 2004). Thus, integrating multiple determinants of patch quality with intraspecific interactions and habitat selection are necessary for understanding species distributions and abundances, community structure and local and regional patterns of biodiversity (Abrams, 2007; Abrams, Cressman, & Krivan, 2007; Chesson, 2000). In the same context, understanding how the cues used to evaluate patch quality are detected, interpreted, and how those cues may interact, is also critical to understanding the dynamics and consequences of decisions made by colonizing organisms.

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AUTHORS' CONTRIBUTIONS

J.R.B. conceived the experiment. J.R.B., M.R.P. and L.L.E. designed and conducted the experiment with input from W.J.R. M.R.P. identified the beetles and analysed the data. M.R.P., J.R.B. and W.J.R. wrote the manuscript.

DATA ACCESSIBILITY

Data available from Dryad Digital Repository https://doi.org/10.5061/dryad.7q3n51j (Pintar, Bohenek, Eveland, & Resetarits, 2018).

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REFERENCES

Abrams, P. A. (2007). Habitat choice in predator-prey systems: Spatial instability due to interacting adaptive movements. *The American Naturalist*, *169*, 581–594. https://doi.org/10.1086/512688

Abrams, P. A., Cressman, R., & Krivan, V. (2007). The role of behavioral dynamics in determining the patch distributions of interacting species. *The American Naturalist*, *169*, 505–518. https://doi.org/10.1086/511963

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2015). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth, UK: PRIMER-E.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 51. https://doi.org/10.18637/jss.v067.i01

Bilton, D. T. (2014). Dispersal in Dytiscidae. In D. A. Yee (Ed.), *Ecology, systematics, and the natural history of predaceous diving beetles (Coleoptera: Dytiscidae)* (pp. 387–407). New York, NY: Springer.

Bilton, D. T., Freeland, J. R., & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, *32*, 159–181. https://doi.org/10.1146/annurev.ecolsys.32.081501.114016

Binckley, C. A., & Resetarits, W. J. Jr (2005). Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biology Letters*, *1*, 370–374. https://doi.org/10.1098/rsbl.2005.0310

Binckley, C. A., & Resetarits, W. J. Jr (2008). Oviposition behavior partitions aquatic landscapes along predation and nutrient gradients. *Behavioral Ecology*, *19*, 552–557. https://doi.org/10.1093/beheco/arm164

Blaustein, L., Kiflawi, M., Eitam, A., Mangel, M., & Cohen, J. E. (2004). Oviposition habitat selection in response to risk of predation in temporary pools: Mode of detection and consistency across experimental venue. *Oecologia*, *138*, 300–305. https://doi.org/10.1007/s00442-003-1398-x

Blaustein, L., & Kotler, B. P. (1993). Oviposition habitat selection by the mosquito, *Culiseta longiareolata*: Effects of conspecifics, food and green toad tadpoles. *Ecological Entomology*, *18*, 104–108. https://doi.org/10.1111/j.1365-2311.1993.tb01190.x

Bohenek, J. R., Pintar, M. R., Breech, T. M., & Resetarits, W. J. Jr (2017). Patch size influences perceived patch quality for colonising *Culex* mosquitoes. *Freshwater Biology*, *62*, 1614–1622. https://doi.org/10.1111/fwb.12972

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*, 37–47. https://doi.org/10.1007/BF00395696

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*, 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x

Brown, J. S., Laundre, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*, 385–399. https://doi.org/10.2307/1383287

Burley, N. T., & Symanski, R. (1998). "A taste for the beautiful": Latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *The American Naturalist*, *152*, 792–802. https://doi.org/10.1086/286209

Carpenter, S. R., Kitchell, J. F., & Hodgson, J. R. (1985). Cascading trophic interactions and lake productivity. *BioScience*, *35*, 634–639. https://doi.org/10.2307/1309989

Carranza, J., & Winn, H. E. (1954). Reproductive behavior of the blackstripe topminnow, *Fundulus notatus*. *Copeia*, *1954*, 273–278. https://doi.org/10.2307/1440041

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7: User manual/tutorial*. Plymouth, UK: PRIMER-E.

Cline, J. M., East, T. L., & Threlkeld, S. T. (1994). Fish interactions with the sediment-water interface. In E. Mortensen, E. Jeppesen, M. Søndergaard & L. Kamp Nielsen (Eds.), *Nutrient dynamics and biological structure in shallow freshwater and brackish lakes* (pp. 301–311). New York, NY: Springer. https://doi.org/10.1007/978-94-017-2460-9_27

Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis*, *150*, 3–17. https://doi.org/10.1111/j.1474-919X.2007.00793.x

Darsie, R. F., & Ward, R. A. (2005). *Identification and geographical distribution of the mosquitoes of North America, North of Mexico*. Gainesville, FL: University Press of Florida.

Drenner, R. W., Smith, J. D., & Threlkeld, S. T. (1996). Lake trophic state and the limnological effects of omnivorous fish. *Hydrobiologia*, *319*, 213–223. https://doi.org/10.1007/BF00013734

Epler, J. H. (2010). *The water beetles of Florida*. Tallahassee, FL: Florida Department of Environmental Protection. Retrieved from http://publicfiles.dep.state.fl.us/dear/labs/biology/biokeys/beetles10.pdf

Eveland, L. L., Bohenek, J. R., Silberbush, A., & Resetarits, W. J. Jr (2016). Detection of fish and newt kairomones by ovipositing mosquitoes. *Chemical Signatures in Vertebrates*, *13*, 247–259. https://doi.org/10.1007/978-3-319-22026-0_18

Ferrari, M. C. O., Wisenden, B. D., & Chivers, D. P. (2010). Chemical ecology of predator-prey interactions in aquatic ecosystems: A review and prospectus. *Canadian Journal of Zoology*, *88*, 698–724. https://doi.org/10.1139/Z10-029

Fretwell, S. D., & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*, 16–36. https://doi.org/10.1007/BF01601953

Fukami, T., & Morin, P. J. (2003). Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, *424*, 423–426. https://doi.org/10.1038/nature01785

Hankison, S. J., & Morris, M. R. (2003). Avoiding a compromise between sexual selection and species recognition: Female swordtail fish assess multiple species-specific cues. *Behavioral Ecology*, *14*, 282–287. https://doi.org/10.1093/beheco/14.2.282

Heithaus, M. R., Wirsing, A. J., Thomson, J. A., & Burkholder, D. A. (2008). A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology*, *356*, 43–51. https://doi.org/10.1016/j.jembe.2007.12.013

Holbrook, S. J., & Schmitt, R. J. (1988). The combined effects of predation risk and food reward on patch selection. *Ecology*, *69*, 125–134. https://doi.org/10.2307/1943167

Houston, A. I., McNamara, J. M., & Hutchinson, J. M. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions Biological Sciences*, *341*, 375–397. https://doi.org/10.1098/rstb.1993.0123

Iversen, L. L., Rannap, R., Briggs, L., & Sand-Jensen, K. (2017). Time-restricted flight ability influences dispersal and colonization rates in a group of freshwater beetles. *Ecology and Evolution*, *7*, 824–830. https://doi.org/10.1002/ece3.2680

Johnson, C. (1969). *Migration and dispersal of insects by flight*. London, UK: Methuen.

Kraft, C. E. (1993). Phosphorus regeneration by Lake Michigan alewives in the mid-1970s. *Transactions of the American Fisheries Society*, *122*, 749–755. https://doi.org/10.1577/1548-8659(1993)122<0749:PRBLMA>2.3.CO;2

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Larson, D. J., Alarie, Y., & Roughley, R. E. (2000). *Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the fauna of Canada and Alaska*. Ottawa, ON: National Research Council of Canada.

Layton, R. J., & Voshell, J. R. (1991). Colonization of new experimental ponds by benthic macroinvertebrates. *Environmental Entomology*, *20*, 110–117. https://doi.org/doi: 10.1093/ee/20.1.110

Leibold, M. A. (1999). Biodiversity and nutrient enrichment in pond plankton communities. *Evolutionary Ecology Research*, *1*, 73–95.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

MacArthur, R. H., & Wilson, E. O. (1967). The theory of island biogeography. *Monographs in Population Biology*, *1*, 1–215.

McCauley, S. J., Rowe, L., & Fortin, M.-J. J. (2011). The deadly effects of “nonlethal” predators. *Ecology*, *92*, 2043–2048. https://doi.org/10.1890/11-0455.1

McPeek, M. A. (2004). The growth/predation risk trade-off: So what is the mechanism? *The American Naturalist*, *163*, E88–E111. https://doi.org/10.1086/382755

Minshall, G. W. (1967). Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, *48*, 139–149. https://doi.org/10.2307/1933425

Moody, A. L., Houston, A. I., & McNamara, J. M. (1996). Ideal free distributions under predation risk. *Behavioral Ecology and Sociobiology*, *38*, 131–143. https://doi.org/10.1007/s002650050225

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*, 1–13. https://doi.org/10.1007/s00442-003-1241-4

Nonacs, P., & Dill, L. M. (1990). Mortality risk vs. food quality trade-offs in a common currency: Ant patch preferences. *Ecology*, *71*, 1886–1892. https://doi.org/10.2307/1937596

Peacor, S. D. (2006). Behavioural response of bullfrog tadpoles to chemical cues of predation risk are affected by cue age and water source. *Hydrobiologia*, *573*, 39–44. https://doi.org/10.1007/s10750-006-0256-3

Pintar, M. R., Bohenek, J. R., Eveland, L. L., & Resetarits, W. J. Jr (2018). Data from: Colonization across gradients of risk and reward: Nutrients and predators generate species-specific responses among aquatic insects. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.7q3n51j

Pintar, M. R., & Resetarits, W. J. Jr (2017a). Context-dependent colonization dynamics: Regional reward contagion drives local compression in aquatic beetles. *Journal of Animal Ecology*, *86*, 1124–1135. https://doi.org/10.1111/1365-2656.12697

Pintar, M. R., & Resetarits, W. J. Jr (2017b). Prey-driven control of predator assemblages: Zooplankton abundance drives aquatic beetle colonization. *Ecology*, *98*, 2201–2215. https://doi.org/10.1002/ecy.1914

Pintar, M. R., & Resetarits, W. J. Jr (2017c). Tree leaf litter composition drives temporal variation in aquatic beetle colonization and assemblage structure in lentic systems. *Oecologia*, *183*, 797–807. https://doi.org/10.1007/s00442-017-3813-8

Pitcher, T. J., Lang, S. H., & Turner, J. A. (1988). A risk-balancing trade off between foraging rewards and predation hazard in a shoaling fish. *Behavioral Ecology and Sociobiology*, *22*, 225–228. https://doi.org/10.1007/BF00300573

Power, M. E. (1990). Effects of fish in river food webs. *Science*, *250*, 811–814. https://doi.org/10.1126/science.250.4982.811

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Reiskind, M. H., Walton, E. T., & Wilson, M. L. (2004). Nutrient-dependent reduced growth and survival of larval *Culex restuans* (Diptera: Culicidae): laboratory and field experiments in Michigan. *Journal of Medical Entomology*, *41*, 650–656. https://doi.org/10.603/0022-2585-41.4.650

Reiskind, M. H., & Wilson, M. L. (2004). *Culex restuans* (Diptera: Culicidae) oviposition behavior determined by larval habitat quality and quantity in southeastern Michigan. *Journal of Medical Entomology*, *41*, 179–186. https://doi.org/10.1603/0022-2585-41.2.179

Relyea, R. A. (2002). Competitor-induced plasticity in tadpoles: Consequences, cues, and connections to predator-induced plasticity. *Ecological Monographs*, *72*, 523–540. https://doi.org/10.1890/0012-9615(2002) 072[0523:CIPITC]2.0.CO;2

Resetarits, W. J. Jr (2001). Colonization under threat of predation: Avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia*, *129*, 155–160. https://doi.org/10.1007/S004420100704

Resetarits, W. J. Jr, & Binckley, C. A. (2009). Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. *Ecology*, *90*, 869–876. https://doi.org/10.1890/08-0613.1

Resetarits, W. J. Jr, & Binckley, C. A. (2013). Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes. *Oecologia*, *173*, 933–946. https://doi.org/10.1007/s00442-013-2644-5

Resetarits, W. J. Jr, & Binckley, C. A. (2014). Species responses of colonising beetles to variation in patch quality, number, and context in experimental aquatic landscapes. *Ecological Entomology*, *39*, 226–235. https://doi.org/10.1111/een.12092

Resetarits, W. J. Jr, Binckley, C. A., & Chalcraft, D. R. (2005). Habitat selection, species interactions, and processes of community assembly in complex landscapes. In M. Holyoak, M. A. Leibold, & R. D. Holt (Eds.), *Metacommunities: Spatial dynamics and ecological communities* (pp. 374–398). Chicago, IL: University of Chicago Press.

Resetarits, W. J. Jr, & Pintar, M. R. (2016). Functional diversity of non-lethal effects, chemical camouflage, and variation in fish avoidance in colonizing beetles. *Ecology*, *97*, 3517–3529. https://doi.org/10.1002/ecy.1593

Rieger, J. F., Binckley, C. A., & Resetarits, W. J. Jr (2004). Larval performance and oviposition site preference along a predation gradient. *Ecology*, *85*, 2094–2099. https://doi.org/10.1890/04-0156

Rosenzweig, M. L. (1991). Habitat selection and population interactions: The search for mechanism. *The American Naturalist*, *137*, S5–S28. https://doi.org/10.1086/285137

Schindler, D. E., Knapp, R. A., & Leavitt, P. R. (2001). Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. *Ecosystems*, *4*, 308–321. https://doi.org/10.1007/s10021-001-0013-4

Semlitsch, R. D., & Boone, M. D. (2010). Aquatic mesocosms. In C. K. Dodd (Ed.), *Amphibian ecology and conservation: A handbook of techniques* (pp. 87–104). Oxford, UK: Oxford University Press.

Sih, A. (1980). Optimal behaviour: Can foragers balance two conflicting demands? *Science*, *210*, 1041–1043. https://doi.org/10.1126/science.210.4473.1041

Silberbush, A., & Blaustein, L. (2008). Oviposition habitat selection by a mosquito in response to a predator: Are predator-released kairomones air-borne cues? *Journal of Vector Ecology*, *33*, 208–211. https://doi.org/10.3376/1081-1710(2008) 33

Silberbush, A., & Blaustein, L. (2011). Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Functional Ecology*, *25*, 1091–1095. https://doi.org/10.1111/j.1365-2435.2011.01873.x

Silberbush, A., Markman, S., Lewinsohn, E., Bar, E., Cohen, J. E., & Blaustein, L. (2010). Predator-released hydrocarbons repel oviposition by a mosquito. *Ecology Letters*, *13*, 1129–1138. https://doi.org/10.1111/j.1461-0248.2010.01501.x

Strom, B. L., Goyer, R. A., & Shea, P. J. (2001). Visual and olfactory disruption by the western pine beetle to attractant baited traps. *Entomologia Experimentalis et Applicata*, *100*, 63–67. https://doi.org/10.1046/j.1570-7458.2001.00848.x

Tatar, M., & Carey, J. R. (1995). Nutrition mediates reproductive trade-offs with age-specific mortality in the beetle *Callosobruchus maculatus*. *Ecology*, *76*, 2066–2073. https://doi.org/10.2307/1941681

Testa, S., & Lago, P. K. (1994). The aquatic Hydrophilidae (Coleoptera) of Mississippi. *Mississippi Agricultural and Forestry Experimental Station Technical Bulletin*, *193*, 1–71.

Thompson, J. N. (2013). *Relentless evolution*. Chicago, IL: University of Chicago Press. https://doi.org/10.7208/chicago/9780226018898.001.0001

Vanni, M. J., Flecker, A. S., Hood, J. M., & Headworth, J. L. (2002). Stoichiometry of nutrient recycling by vertebrates in a tropical stream: Linking biodiversity and ecosystem function. *Ecology Letters*, *5*, 285–293. https://doi.org/10.1046/j.1461-0248.2002.00314.x

Vonesh, J. R., Kraus, J. M., Rosenberg, J. S., & Chase, J. M. (2009). Predator effects on aquatic community assembly: Disentangling the roles of habitat selection and post-colonization processes. *Oikos*, *118*, 1219–1229. https://doi.org/10.1111/j.1600-0706.2009.17369.x

Wellborn, G. A., Skelly, D. K., & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, *27*, 337–363. https://doi.org/10.1146/annurev.ecolsys.27.1.337

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology*, *69*, 1352–1366. https://doi.org/10.2307/1941633

Zalom, F. G., Grigarick, A. A., & Way, M. O. (1979). Seasonal and diel flight periodicities of rice field Hydrophilidae. *Environmental Entomology*, *8*, 938–943. https://doi.org/doi: 10.1093/ee/8.5.938

Zera, A. J., & Denno, R. F. (1997). Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology*, *42*, 207–230. https://doi.org/10.1146/annurev.ento.42.1.207

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