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Habitat selection determines abundance, richness and species composition of beetles in aquatic communities

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Distribution and abundance patterns at the community and metacommunity scale can result from two distinct mechanisms. Random dispersal followed by non-random, site-specific mortality (species sorting) is the dominant paradigm in community ecology, while habitat selection provides an alternative, largely unexplored, mechanism with different demographic consequences. Rather than differential mortality, habitat selection involves redistribution of individuals among habitat patches based on perceived rather than realized fitness, with perceptions driven by past selection. In particular, habitat preferences based on species composition can create distinct patterns of positive and negative covariance among species, generating more complex linkages among communities than with random dispersal models. In our experiments, the mere presence of predatory fishes, in the absence of any mortality, reduced abundance and species richness of aquatic beetles by up to 80% in comparison with the results from fishless controls. Beetle species' shared habitat preferences generated distinct patterns of species richness, species composition and total abundance, matching large-scale field patterns previously ascribed to random dispersal and differential mortality. Our results indicate that landscape-level patterns of distribution and species diversity can be driven to a large extent by habitat selection behaviour, a critical, but largely overlooked, mechanism of community and metacommunity assembly.

Keywords: community structure; habitat selection; metacommunities; non-lethal effects; species distributions; species interactions

1. INTRODUCTION

Identifying the underlying mechanisms that produce patterns of biodiversity is a defining goal of ecology. However, patterns of distribution and diversity may ultimately derive from several alternative mechanisms (Levin 1992). Classic patterns of species segregation between predators and highly vulnerable prey can result from two mechanisms differing in their underlying processes of dispersal and colonization. Random (undirected) dispersal followed by differential mortality (species sorting) is commonly assumed in community and metacommunity models. Immigration rate is largely a function of patch area and distance from sources of colonists (van Baalen & Hochberg 2001; Leibold *et al.* 2004) and patterns of species distribution are a function of differential mortality among habitat patches. In contrast, habitat selection theory emphasizes the ability of species to disperse and colonize patches with the highest expected fitness (Fretwell & Lucas 1970; Pulliam & Danielson 1991; Rosenzweig 1991; Resetarits 1996; Morris 2003) and resulting patterns of distribution are a function of spatial redistribution of individuals among habitat patches (Resetarits *et al.* in press). Random dispersal followed by differential mortality is the reigning paradigm in community ecology, while the role of habitat selection at the community (and metacommunity—*sensu lato* Leibold *et al.* 2004) level remains largely unexplored.

Habitat selection can affect population growth rate, abundance and persistence for individual species, but community and metacommunity-level consequences depend on its prevalence among dispersing and colonizing species and how niche axes are partitioned by regional species pools (Pulliam & Danielson 1991; Spencer *et al.* 2002). If habitat selection is prevalent, the very presence of predators, for example, can structure both local communities and regional metacommunities by simultaneously altering the dispersal and colonization of multiple prey species. If a niche axis is distributed (or perceived) as a state variable (e.g. predator presence or absence), performance optima for numerous species can overlap in the same habitat type (Resetarits & Wilbur 1989; Rosenzweig 1991), generating positive and negative covariances among prey species as a result of shared or complementary patterns of avoidance or attraction (Resetarits *et al.* in press). A critical distinction is that species interactions that have manifested in habitat selection do not require spatial co-occurrence (functioning alternately via behavioural spatial segregation) and thus operate both within communities and at the metacommunity scale (Resetarits 2005).

Multispecies habitat selection generates very different ecological consequences compared with random dispersal and differential mortality because species distributions are based on the redistribution of individuals rather than mortality, and on perceived rather than actual fitness. Perceptions of fitness are presumably driven by habitat interactions in the species' evolutionary past (Resetarits & Wilbur 1989). The distinction between redistribution of individuals versus differential mortality becomes especially critical as metapopulation and metacommunity models move beyond simple patch occupancy to consider variation in abundance. Thus, classic ecological explanations may no longer hold if, for example, immigration and extinction rates are functions of specific habitat characteristics that attract or repel colonists and generate local variation in population size, rather than being simple functions of patch size and distance.

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Table 1. Summary of analyses. num, numerator; den, denominator.

experiment 1					
source	Wilks' λ	F	num. d.f.	den d.f.	p
block	0.098	6.16	10	28	<0.0001
habitat complexity	0.754	2.28	2	14	0.1384
fishes	0.184	31.11	2	14	<0.0001
habitat complexity × fishes	0.86	1.14	2	14	0.3482
source	d.f.	SS	MS	F	p
abundance					
block	5	1339.3	267.9	9.27	0.0004
habitat complexity	1	20.2	20.2	0.70	0.4167
fishes	1	1837.5	1837.5	63.56	<0.0001
habitat complexity × fishes	1	32.7	32.7	1.13	0.3046
species richness					
block	5	35.00	7.00	6.43	0.0022
habitat complexity	1	0.67	0.67	0.61	0.4461
fishes	1	54.00	54.00	49.59	<0.0001
habitat complexity × fishes	1	0.00	0.000	0.00	1.0000
experiment 2					
source	Wilks' λ	F	num. d.f.	den d.f.	p
block	0.408	0.94	6	10	0.5068
treatment	0.15	3.95	4	10	0.0355
contrast					
control versus *Enneacanthus*	0.161	13.03	2	5	0.0104
control versus *Aphredoderus*	0.740	0.88	2	5	0.4717
Enneacanthus versus *Aphredoderus*	0.258	7.19	2	5	0.0338
abundance					
source	d.f.	SS	MS	F	p
block	3	376.7	125.6	0.74	0.5648
treatment	2	3004.7	1502.3	8.88	0.0161
contrast	d.f.	contrast SS	MS	F	p
control versus *Enneacanthus*	1	2738	2738.0	16.18	0.0069
control versus *Aphredoderus*	1	144.5	144.5	0.85	0.3911
Enneacanthus versus *Aphredoderus*	1	1624.5	1624.5	9.60	0.0212
species richness					
source	d.f.	SS	MS	F	p
block	3	3.67	1.22	0.57	0.6542
treatment	2	71.17	35.58	16.64	0.0036
contrast	d.f.	contrast SS	MS	F	p
control versus *Enneacanthus*	1	66.1	66.1	30.92	0.0014
control versus *Aphredoderus*	1	4.5	4.5	2.10	0.1971
Enneacanthus versus *Aphredoderus*	1	36.1	36.1	16.89	0.0063

The distribution of predatory fishes is a critical determinant of the landscape-level distribution and abundance of many aquatic taxa (Wellborn *et al.* 1996). Common aquatic beetles (Coleoptera) are typically less abundant, and rare species are absent, in habitats that contain fishes. Traditionally, reduced abundance, biomass and richness were attributed to differential mortality (Weir 1972; Healey 1984; Fairchild *et al.* 2000). However, this pattern can also be generated by multiple species selecting ponds based on the presence or absence of fishes (Resetarits 2001). We conducted two experiments quantifying how the non-lethal presence of predatory fishes affects mean abundance and species richness of colonizing aquatic beetles.

2. METHODS

(a) *Experiment 1*

We crossed the non-lethal presence or absence of one *Enneacanthus obesus* (Centrarchidae; mean mass: 2.47 g) with the presence or absence of supplemental habitat complexity (artificial substrates). Habitat complexity often reduces predation, thus, we tested beetle responses to a known predator (Graham & Vrijenhoek 1988), preference for complex habitats, and whether preferences were affected by fishes. We established 24 experimental ponds (wading pools: 1.50 × 0.29 m; 300 l) arranged in six linear blocks (*ca* 20 m apart) of four pools each (*ca* 1.3 m apart) that were surrounded by hardwood and pine forest in a field in Chesapeake VA, USA. On 8 July we covered ponds with a tight-fitting fibreglass screen (2 mm^2) to prevent premature colonization by insects and filled pools with tap water. Two days later, we added randomized aliquots of 0.4 kg of dried leaf litter and 1.0 l of zooplankton and phytoplankton. Supplemental habitat complexity consisted of 600 plastic cable ties attached to a plastic grid comprising 600 1 cm^2 sections. The four treatments (presence or absence of predators × presence or absence of habitat complexity) were randomly assigned to pools within blocks.

On 10 July, fishes were placed under screens, screens pushed underwater and habitat complexity added atop the lids. This eliminated physical interactions between predators and beetles but allowed chemical communication. Treatments lacking habitat complexity had equal amounts of unassembled cable ties and equal numbers of grids placed under the screen. Beetles were collected from the pools on 27 July and preserved in 95% ethanol.

We examined effects of block and treatment on mean beetle abundance (total) and mean species richness. A single MANOVA was performed using SAS for Windows version 8.0 (type III SS, $\alpha = 0.05$) followed by univariate ANOVAs (table 1).

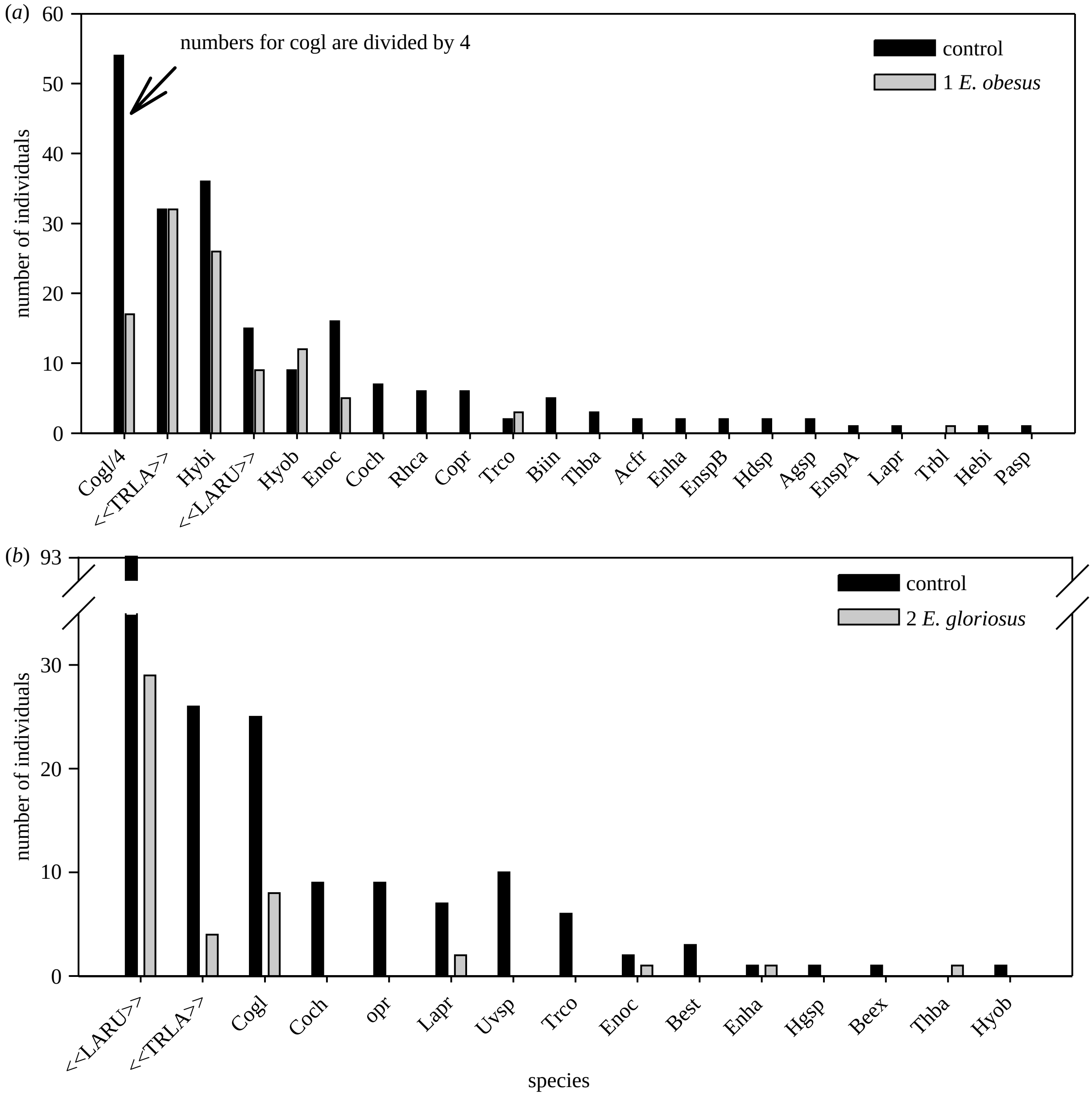

Figure 1. Number of beetles (table 2) in controls and experimental ponds containing (*a*) one caged, *Enneacanthus obesus* and (*b*) two caged *Enneacanthus gloriosus*. Avoidance response of *Laccophilus rufus* (LARU) and *Tropisternus lateralis* (TRLA) only in experiment 2 probably indicates a threshold response to fish density (Rieger *et al.* 2004; see text). Both experiments contained additional, non-significant treatments that were excluded for clarity (see table 1).

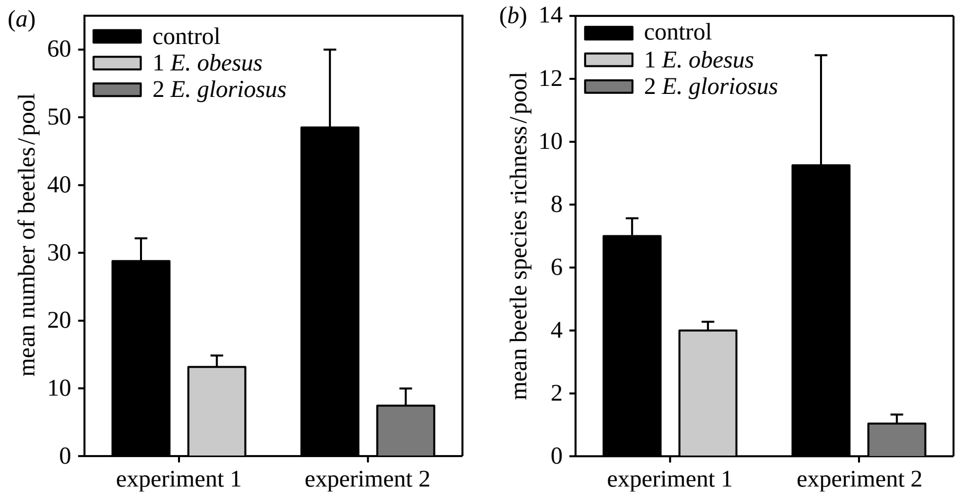

Figure 2. Effects of habitat selection on (*a*) mean beetle abundance and (*b*) mean species richness.

Table 2. Codes and corresponding scientific names used in figure 1.

code	name	code	name
Cogl	*Copelatus glyphicus*	Enha	*Enochrus hamiltoni*
Trla	*Tropisternus lateralis*	EnspB	*Enochrus* sp. B
Hybi	*Hydaticus bimarginatus*	Hdsp	*Hydrochus* sp.
Laru	*Laccophilus rufus*	Agsp	*Agabus* sp.
Hyob	*Hydrochara obtusata*	EnspA	*Enochrus* sp. A
Enoc	*Enochrus ochraceus*	Lapr	*Laccophilus proximus*
Coch	*Copelatus chevrolati*	Trbl	*Tropisternus blatchleyi*
Rhca	*Rhantus calidus*	Hebi	*Helocombus bifidus*
Copr	*Copelatus princeps*	Pasp	*Paracymus* sp.
Trco	*Tropisternus collaris*	Uvsp	*Uvarus* sp.
Biin	*Bidessonotus inconspicuus*	Best	*Berosus striatus*
Thba	*Thermonectus basillaris*	Hgsp	*Hygrotus* sp.
Acfr	*Acilius fraternus*	Beex	*Berosus exiguus*

(b) *Experiment 2*

We used the same methodology to establish 12 experimental ponds in four blocks. On 28 August we randomly assigned three treatments to ponds within blocks: two *Enneacanthus gloriosus* (mean mass 2.69 g), two *Aphredoderus sayanus* (Aphredoderidae; 4.06 g) and fishless controls. Aphredoderidae is a monotypic family and was included because it is a known predator of beetles (Sheldon & Meffe 1993) and represents the only species (or family), out of seven species (five families) tested, that is not avoided by ovipositing tree frogs (Resetarits & Wilbur 1989; Binckley & Resetarits 2003). Beetles were collected weekly for three weeks. Analysis consisted of a MANOVA and non-orthogonal multivariate and univariate contrasts to examine differences between treatments.

3. RESULTS

Figure 1 shows the distribution of 783 individuals of 26 beetle species between pools with and without *Enneacanthus*. The reduction in the abundance of common species and the elimination of rare species was generated behaviourally (figure 1; table 1). Of the 26 species, only nine colonized ponds with *Enneacanthus* while only a single species (*Tropisternus blatchleyi*), represented by a single individual, occurred solely with fishes. Both mean species richness/pool and mean abundance/pool were reduced by up to 80% by the non-lethal presence of fishes (figure 2; table 1), with the magnitude of effects increasing in experiment 2.

In experiment 1, habitat complexity had no effect and there was no interaction between habitat complexity and the presence or absence of fishes. In experiment 2, responses to *A. sayanus* did not differ significantly from controls for any response variables. The atypical response to *A. sayanus* by both beetles and tree frogs (Binckley & Resetarits 2003), which are both readily consumed by this small, benthic fish, is under further investigation.

4. DISCUSSION

Habitat selection theory suggests that, if habitats are hierarchical in suitability, colonization of less suitable habitats occurs only as density increases in preferred sites. Even the least suitable sites are occupied at saturation densities, because the fitness in a poor site exceeds that of a good site where resources are already monopolized (Fretwell & Lucas 1970). This density-dependant process restricts the ability of field patterns alone to establish primary habitat preferences or determine the ultimate processes leading to observed species distributions (but see Morris 2003). Our experimental approach demonstrated that the presence of small predatory fishes significantly reduced the mean abundance and species richness of beetles via habitat selection behaviour alone. Aquatic beetles had clear habitat preferences for fishless ponds and the resulting patterns of species richness and abundance matched those reported by large-scale field surveys (Weir 1972; Healey 1984; Fairchild *et al.* 2000). Although we did not test specifically for density-dependence habitat choice (*sensu* the ideal free distribution; Fretwell & Lucas 1970), it is certainly possible that the presence of common species in pools with fishes reflects a response to increased density in preferred (fishless) pools, as suggested by data on tree frogs (Binckley & Resetarits 2003).

Interestingly, we observed decreased abundance of several common beetle species in ponds with fishes only in experiment 2, in which fish identity changed and both density and fish biomass were two times higher. We suspect this, and the stronger overall response, are a consequence of density rather than the relatively subtle change in predator identity, as one of the common beetles, *Tropisternus lateralis*, shows essentially equivalent responses to two other centrarchid species at similar densities (Resetarits 2001). In addition, we previously identified fish density thresholds that trigger avoidance (Rieger *et al.* 2004) and established the functional equivalence of fish predators from four families (except *A. sayanus*) with respect to behavioural avoidance in tree frogs (Binckley & Resetarits 2003). Thus, our experiments, which used low fish densities relative to nature, constitute a conservative estimate of the effects of habitat selection on community structure and substantiate a growing body of work suggesting that habitat selection is a primary mechanism driving the distribution and abundance of species in aquatic systems (Resetarits & Wilbur 1989; Blaustein 1999; Åbjörnsson *et al.* 2002; Binckley & Resetarits 2003; Kiflawi *et al.* 2003; Morris 2003; Rieger *et al.* 2004; Resetarits 2005; Resetarits *et al.* in press). Our results also affirm a counter-intuitive process of decreasing local mortality with increasing predator abundance for species that detect and avoid fishes (figure 2; Abrams 1993; Rieger *et al.* 2004).

While both local and larger scale regional processes influence population and community structure, ecologists lack a critical understanding of how processes operating at different scales interact to influence patterns of distribution and diversity (Shurin & Allen 2001; Kneitel & Miller 2003; Leibold *et al.* 2004; Resetarits 2005). Habitat selection generates such interactions between local and regional processes because rates and magnitudes of dispersal from or into local communities depend on specific habitat characteristics (e.g. predator presence or absence; Resetarits in press). Species interactions thus operate at two distinct spatial scales: locally within communities of spatially co-occurring species and regionally among species residing in spatially discrete local communities. This is strikingly different from the random dispersal/differential mortality paradigm where all interactions occur locally. In our study, two species of *Enneacanthus* interacted strongly with individuals of numerous beetle species, without co-occurring or causing direct mortality, by invoking a behavioural redistribution among habitats. Such cryptic, phantom interactions are another form of behavioural non-lethal effects that, along with the 'ecology of fear' (Brown *et al.* 1999) and behavioural trait-mediated interactions (Werner & Peacor 2003), constitute a largely missing element in community ecology.

Habitat selection is a critical process in community assembly and is particularly germane to metacommunity dynamics because it elevates the probability and intensity of entirely different sets of local interactions among species forced to spatially co-occur due to shared habitat preferences. Thus, regional landscapes are behaviourally partitioned into different habitat types occurring in unique spatial configurations, resulting in complex patterns of linkage among communities (Resetarits *et al.* in press). When the important aspects of habitat include other species whose distributions vary in space and time, such as mobile predators, habitat selection may be especially critical and the resulting spatial and temporal dynamics of species distributions and (meta)community structure may be especially volatile (Resetarits & Wilbur 1989; Blaustein 1999; Brown *et al.* 1999; Resetarits 2005).

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