

Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities

Christopher A. Binckley · William J. Resetarits Jr

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Abstract The specific dispersal/colonization strategies used by species to locate and colonize habitat patches can strongly influence both community and metacommunity structure. Habitat selection theory predicts nonrandom dispersal to and colonization of habitat patches based on their quality. We tested whether habitat selection was capable of generating patterns of diversity and abundance across a transition of canopy coverage (open and closed canopy) and nutrient addition by investigating oviposition site choice in two treefrog species (*Hyla*) and an aquatic beetle (*Tropisternus lateralis*), and the colonization dynamics of a diverse assemblage of aquatic insects (primarily beetles). Canopy cover produced dramatic patterns of presence/absence, abundance, and species richness, as open canopy ponds received 99.5% of propagules and 94.6% of adult insect colonists. Nutrient addition affected only *Tropisternus* oviposition, as females oviposited more egg cases at higher nutrient levels, but only in open canopy ponds. The behavioral partitioning of aquatic landscapes into suitable and unsuitable habitats via habitat selection behavior fundamentally alters how communities within larger ecological landscapes (metacommunities) are linked by dispersal and colonization.

Keywords Behavior · Colonization · Dispersal · Productivity · Oviposition

Introduction

Processes operating at larger spatial scales can profoundly affect ecological dynamics (Ricklefs 1987; Holt 1993; Leibold et al. 2004). For example, communities are often connected by multispecies dispersal and colonization into larger spatial units or metacommunities (Holyoak et al. 2005). Here, community structure is determined by how processes occurring within a community (predation, competition, abiotic effects, etc.) interact with rates of multispecies dispersal and colonization (Leibold et al. 2004; Holyoak et al. 2005). It is thus critical to understand how species locate and colonize habitat patches, as different strategies (passive dispersal, philopatry, habitat selection) greatly impact habitat-specific rates of colonization and the magnitude of linkages among communities (Hanski and Singer 2001; Holt and Barfield 2001; Binckley and Resetarits 2005; Resetarits et al. 2005).

Habitat selection theory predicts highly nonrandom dispersal to and colonization of patches that provide the greatest expected fitness (Fretwell and Lucas 1970; Sutherland 1996; Van Baalen and Hochberg 2001; Morris 2003). Distribution and abundance patterns are behaviorally generated, as rates and magnitudes of dispersal/colonization depend primarily on local patch characteristics (Resetarits and Wilbur 1989; Rosenzweig 1991; Blaustein 1999; Binckley and Resetarits 2003). When these characteristics are distributed or perceived as a binary variable (e.g., open/closed forest canopy, predators/no predators), performance optima for numerous species must overlap in the same habitat type (Rieger et al. 2004). If distributed and

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C. A. Binckley (✉)
Department of Biological Sciences,
Old Dominion University, Norfolk, VA 23529, USA
e-mail: cbinckle@odu.edu

W. J. Resetarits Jr
School of Biological Sciences,
University of Southampton, Southampton, SO16 7PX, UK

perceived as a continuous variable, behavioral species sorting takes on even greater complexity (Rieger et al. 2004). In either case, habitat selection fundamentally changes the degree to which communities are linked by dispersal and colonization relative to other dispersal strategies, as patches of the same habitat type will be strongly connected via shared species relative to those comprising different habitat types (Binckley and Resetarits 2005; Resetarits et al. 2005).

Freshwater aquatic communities (e.g., wetlands, ponds, lakes) are embedded within larger terrestrial landscapes and are linked both to each other and the surrounding terrestrial matrix by species with complex life cycles (Wellborn et al. 1996; Wilbur 1997). These mosaics of aquatic communities can be conceptualized as metacommunities, with individual aquatic patches comprising local communities with their own set of intrinsic processes (Shurin 2001; Kneitel and Miller 2003; Resetarits et al. 2005). In addition to considerable intrinsic variation, characteristics of the surrounding terrestrial habitat can be highly variable and have dramatic effects on local aquatic communities (Skelly et al. 1999; Werner and Glennemeier 1999). Despite such variation, the performance of numerous species, and resulting patterns of distribution, abundance, and diversity, are strongly affected by and correlated with forest canopy cover (Werner and Glennemeier 1999; Skelly et al. 1999; Grether et al. 2001).

There is growing concern over how large-scale modification of terrestrial vegetation (see Caspersen et al. 2000; Chen et al. 2006) affects aquatic systems (Skelly et al. 1999; 2002; Hill et al. 2001; Halverson et al. 2003; Rubbo and Kiesecker 2004). Predicting these effects requires a mechanistic understanding of how observed changes in distribution and abundance are generated in response to changing canopy cover.

We examined oviposition site choice in natural populations of two species of treefrog (*Hyla chrysoscelis* and *H. squirella*), and an aquatic hydrophilid beetle (*Tropisternus lateralis*), as well as the colonization dynamics of a diverse assemblage of aquatic insects (primarily beetles), to assess the importance of habitat selection as a mechanism underlying changes in species distribution and abundance with changes in canopy cover. We specifically asked whether open versus closed canopy sites represent distinct habitat types in terms of differences in colonization, and whether any preferences for canopy type were altered by variation in nutrient levels (productivity). Variation in productivity, primarily as a result of changes in insolation, is a major correlate of change in canopy cover (Hill et al. 2001). However, productivity also varies with nutrient availability within a canopy level. Thus, we manipulated habitat quality by establishing experimental ponds in areas of open and closed forest canopy, and by manipulating nutrient levels among patches within each canopy type.

Materials and methods

Study organisms

Our experiment examined the degree to which canopy coverage and nutrient addition affected oviposition in two species of anurans and an aquatic beetle. We also quantified the colonization dynamics of a diverse suite of adult aquatic insects comprised primarily of coleopterans as well as several common hemipterans (Fig. 3). Numerous other insects colonize (e.g., smaller beetles, hemipterans, mites, surface-dwelling dipterans) and/or oviposit in the pools (e.g., odonates, dipterans, etc.), but these were not quantified due to the difficulty involved in identifying eggs and accurately quantifying adults, eggs and larvae.

Hyla chrysoscelis and *H. squirella* are terrestrial/arbooreal treefrogs that deposit eggs in ponds as floating surface rafts (*H. chrysoscelis*) or as small clusters or strings (*H. squirella*) after heavy rains during the late spring and summer. Eggs hatch into herbivorous larvae that forage in their natal pond until metamorphosing into a terrestrial juvenile (Wilbur 1997). For *Hyla*, oviposition site selection is a specific form of habitat selection where adults choose habitat for their offspring (Blaustein 1999; Binckley and Resetarits 2003). These species are two of the most abundant anurans on the Coastal Plain of Virginia, where the elevation and lack of topography at our study site (approximately 3–4 m above sea level) combined with natural and anthropogenic disturbances (fire, agriculture, timber harvest, field abandonment, etc.) generate numerous open and closed canopy wetlands. However, both species primarily recruit from open canopy ponds, a pattern that may be driven by either behavioral avoidance or early larval mortality.

Aquatic beetles are abundant in local ponds from early spring to late fall. They feed and reproduce in the water and adults can emigrate from ponds if local conditions change (e.g., pond drying). Many aquatic insect species, including coleopterans, show increased abundance and richness in more open canopy ponds (Matta 1979; Nilsson and Svensson 1995; Palik et al. 2001; Fairchild et al. 2003; Tuno et al. 2005). Most species at our study site are predaceous diving beetles (Dytiscidae), with carnivorous adults and larvae, or water scavenger beetles (Hydrophilidae), with primarily omnivorous or herbivorous adults (grazer/scavengers) and carnivorous larvae. For example, *Tropisternus lateralis* is a hydrophilid beetle with obligate aquatic adults, larvae, and egg cases (Zalom et al. 1979; Resetarits 2001). Adult dispersal occurs after an obligate terrestrial pupal stage that occurs along the periphery of ponds and adults disperse aerially amongst ponds for feeding and reproduction (Zalom et al. 1979). Females lay conspicuous silken egg cases (3–4 mm) containing 12–24 eggs that hatch into predaceous larvae (Zalom et al. 1979; Zalom and Grigarick

1980; Resetarits 2001). Egg deposition occurs at our study site from early April to October with most occurring from June–August (personal observation). It is not clear whether adults modify their habitat use prior to oviposition or simply deposit egg cases in the same localities where they are foraging (see Mayhew 1998).

Experimental design

The nature of our question requires the use of experimental mesocosms to control for some of the local factors (quantity, quality, and age of both water and substrate, other competitors and predators), and regional factors (the number and spatial arrangement of patches of each potential habitat type) that most often co-vary with canopy coverage and confound efforts to identify causal mechanisms (Werner and Glennemeier 1999; Skelly et al. 1999, 2002; Halverson et al. 2003).

We established 24 experimental ponds in four spatial blocks of six ponds each at the Naval Security Group Activity Northwest (NSGANW) base in Chesapeake, VA. Ponds were cattle watering tanks ≈ 1.65 m in diameter, 0.61 m in depth, and 1000 L in total volume. Each block was established at a field/forest ecotone with three ponds located 3–4 m into the woods (closed canopy) and three located the same distance into the field (open canopy). Individual ponds in the same block and canopy type were ≈ 1.5 m from each other in a triangular arrangement, and blocks were located ≈ 30 m apart. Forest was ≈ 25 years post-agricultural abandonment and dominated by red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*), while the field was regularly mowed. Our manipulations represent the endpoints of a gradient of canopy cover, from fully open canopy in our oldfields to essentially fully closed canopy in our forest sites. In natural systems, all possible positions between these two extremes are possible.

We covered ponds with tight-fitting fiberglass screen lids (2×2 mm mesh) before filling with tap water and adding 1.0 kg of dried leaf litter on 29–30 June. Ponds aged for three days before 1.0 L aliquots of a phytoplankton/zoo-plankton mixture were added to all tanks by randomly selecting a block and then randomly selecting a pond within that block prior to addition. On 5 July, we randomly assigned (see above) three nutrient treatments (0, 30, and 60 g of Forti-Diet[®] rabbit chow pellets) to ponds within each canopy type. Screen lids were pushed down into the water on 8 July to allow colonization. We did not quantify productivity, but periphyton and phytoplankton responded rapidly to nutrient addition (see Leibold and Wilbur 1992; Blaustein and Kotler 1993; Skelly et al. 2002). Ponds were checked daily for oviposition, and all eggs/egg cases were removed and counted. On 30 July, at termination, all larger

adult aquatic insects located above the submerged screens were collected from each experimental pond using small hand-held dipnets. Small beetles, insect eggs, and other larval and adult insects that could pass through the screen mesh were not quantified. All aquatic insects collected (see Fig. 3) were placed in alcohol and identified to species when possible.

We utilized a split-plot design with canopy as the whole plot factor and nutrient addition as the subplot factor, and examined the effect of block, canopy, nutrients, and the canopy \times nutrient interaction on five response variables: number of *H. squirella* eggs, number of *H. chrysoscelis* eggs, number of *T. lateralis* egg cases deposited, and number and species richness of aquatic insects. Univariate split-plot ANOVAs (type III SS and $\alpha = 0.05$) were performed for each response variable, and count data were square-root-transformed prior to analysis to meet ANOVA assumptions. Considerable heterogeneity of variances persisted (variances correlated with means as a result of all of the closed canopy means being near zero), but this did not affect the overall results.

Results

Canopy coverage was the dominant factor explaining the spatial distribution of propagules and adult colonists for all species (Figs. 1, 2, 3; Table 1). A total of 83,481 *H. squirella* eggs (≈ 120 individual clutches, based on site specific data; D. Chalcraft, personal communication), 67,401 *H. chrysoscelis* eggs (≈ 80 individual clutches based on site specific data; D. Chalcraft, personal communication), and 422 *T. lateralis* egg cases were collected during the experiment. Not a single *H. squirella* egg or *T. lateralis* egg case was deposited in a closed canopy pond, and these sites only received 7,301 *H. chrysoscelis* eggs (10.8% of species total) (Fig. 1). Thus, 99.5% of the total reproductive effort of our three focal species was focused on open canopy ponds. The only significant nutrient addition main effect or nutrient by canopy interaction was produced by *T. lateralis*, which deposited significantly more egg cases at higher nutrient levels (30 and 60 g) in open canopy ponds (Fig. 1, Table 1). Neither species of *Hyla* responded to nutrient addition (Fig. 1, Table 1), which was surprising given the increased algal growth in tanks with added nutrients (personal observation), and its known effect on larval growth (Leibold and Wilbur 1992; Blaustein and Kotler 1993; Skelly et al. 2002).

Our samples of aquatic insects were composed of 725 individuals of 28 different species (Figs. 2, 3), 705 individuals of 25 species of Coleoptera, and 20 individuals of three species of Hemiptera. Almost all individuals (94.6%) colonized open canopy ponds, resulting in significantly higher

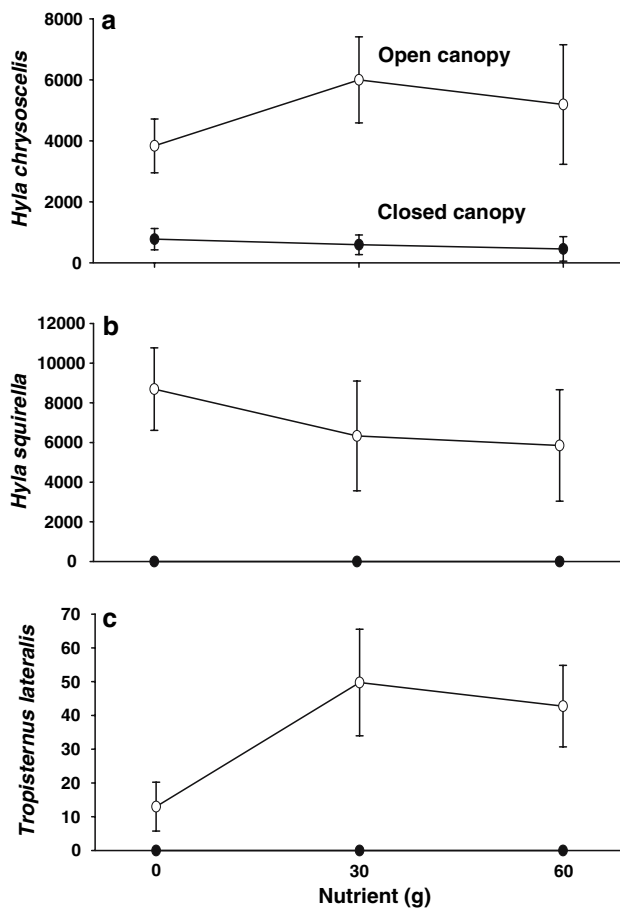


Fig. 1a–c Oviposition site selection, measured as mean number (\pm SE) of (a, b) eggs or (c) egg cases of a *Hyla chrysochloris*, b *H. squirella* and c *Tropisternus lateralis* in open (open circles) or closed (filled circles) canopy experimental ponds with 0, 30, or 60 g of added nutrients

mean abundance and species richness (Figs. 2, 3, Table 1). Mean insect abundances varied almost 20-fold, with a mean (\pm 1 SE) of 62.4 (8.6) individuals captured in open ponds versus 3.2 (0.53) in closed canopy sites. Similarly, mean species richness (\pm 1 SE) varied sevenfold from 14.4 (1.2) species in open localities to 2.1 (0.32) in closed canopy ponds. These dramatic effects of canopy were not modified by nutrient addition (Table 1). The distribution of the 28 insect species between open and closed canopy are illustrated in Fig. 3; 24 of 28 species were more abundant in open canopy ponds, most overwhelmingly so.

Discussion

Canopy cover imposed a strong behavioral filter on both treefrogs and aquatic insects, producing discrete, habitat-specific spatial patterns of presence/absence, abundance and species richness (Figs. 1, 2, 3). For these assemblages,

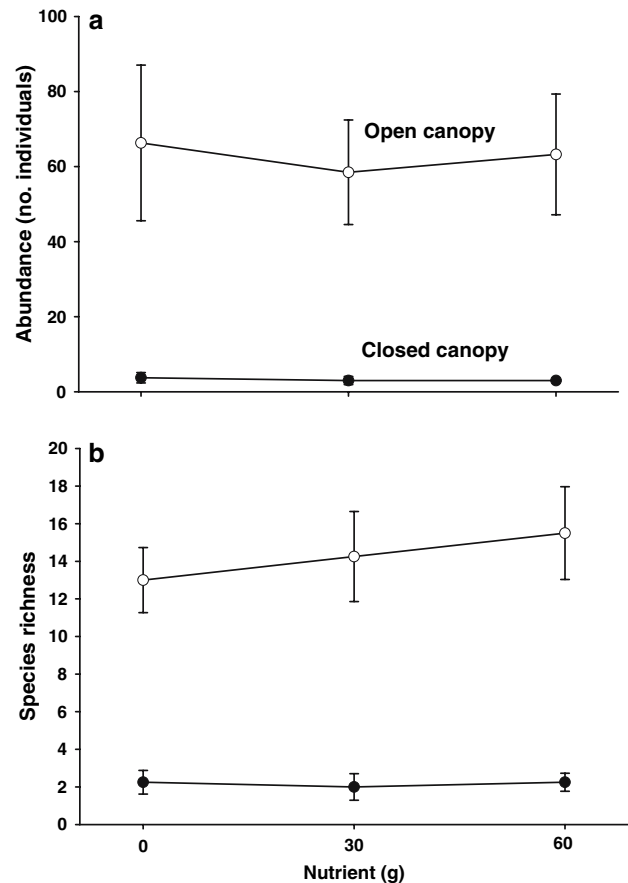
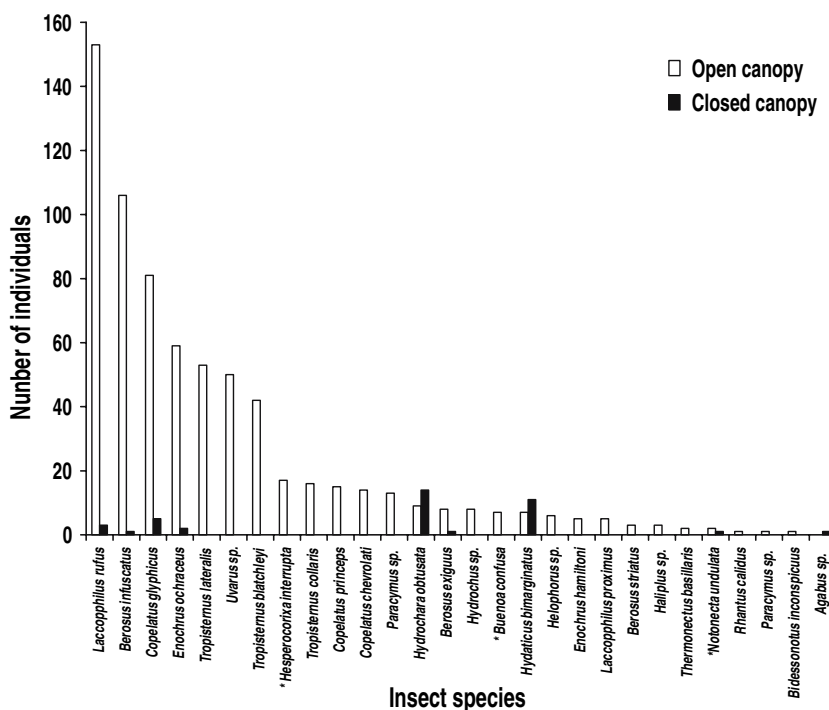


Fig. 2a–b a Abundance and b species richness (mean \pm SE) of aquatic insects in open (open circles) or closed (filled circles) canopy experimental ponds with 0, 30, or 60 g of added nutrients

open and closed canopy ponds clearly represent distinct habitat types from the perspective of oviposition and colonization. Preference for open canopy sites was shared by all three ovipositing species, as well as by adults of 24 of 28 insect species, while *T. lateralis* further demonstrated some ability to behaviorally partition open canopy sites based on expected productivity (Figs. 1, 2, 3). Our data suggest that distinct distribution and diversity patterns of aquatic taxa correlated with canopy coverage (Nilsson and Svensson 1995; Skelly et al. 1999; Palik et al. 2001; Fairchild et al. 2003; Tuno et al. 2005) can be generated primarily by habitat selection rather than post-colonization mortality. The strength of habitat selection in response to canopy cover and resulting patterns of distribution and abundance rival those elicited by predatory fish (e.g., Binckley and Reseraris 2003, 2005; Brodin et al. 2006), demonstrating the existence of multiple, potentially interacting, behavioral sieves operating among discrete aquatic communities.

In contrast, the general paucity of responses to nutrient addition was surprising (Figs. 1, 2), especially for treefrogs with their herbivorous larvae. The level of added nutrients was substantial relative to similar experiments,

Fig. 3 Number of individuals of 28 insect species [three species of Hemiptera (denoted with asterisks) and 25 species of Coleoptera] collected from open (white bars) and closed (black bars) canopy experimental ponds at the termination of the experiment. Experimental ponds were accessible to insect colonists for three weeks



and although productivity was not measured directly, periphyton and phytoplankton responded dramatically to increased nutrients with rapid growth of algae on the walls of the tanks and reduced water clarity due to elevated densities of phytoplankton (sensu Leibold and Wilbur 1992; see also Blaustein and Kotler 1993; Skelly et al. 2002). Adult *Hyla*, unlike *Tropisternus*, may lack the ability to detect elevated resources/productivity directly, or perhaps nutrient addition did not produce productivity differences detectable to *Hyla* given the short duration of the experiment. Alternatively, productivity may not actually increase fitness if correlated factors, such as predator-induced mortality from larval *T. lateralis*, negate potential fitness gains (Fig. 1). Longer term experiments are needed that directly manipulate and measure productivity, in conjunction with larval performance experiments, to determine how and why species differentially respond to productivity gradients. However, avoiding closed canopy sites generally results in colonization of ponds with higher productivity, and avoidance of fish predators (Binckley and Resetarits 2003) likely places individuals in ephemeral ponds with predicted higher productivity (Odum et al. 1995; Williams 2006). Individuals utilizing these joint criteria consequently colonize sites on the upper end of the productivity spectrum without having to actively search out these sites. Nonetheless, *Hyla* females failed to distinguish even among open canopy ponds with potentially different levels of productivity, and we have replicated these results in other experiments that ran over an entire summer (C.A. Binckley and W.J. Resetarits Jr, submitted).

The mechanism(s) by which variation in canopy coverage is assessed prior to colonization/oviposition remains unknown. Ponds located across canopy gradients consistently differ in numerous local abiotic variables such as temperature, dissolved oxygen, reflectance etc. (Werner and Glennemeier 1999; Bernath et al. 2002). Canopy itself could be the cue used to assess habitat quality as it generates, and thus is reliably correlated with, these local abiotic differences. A simple rule-based search strategy such as “when colonizing/ovipositing don’t use the forest” greatly reduces searching costs (Maynard Smith 1982), since little time would be wasted traveling among unsuitable, closed canopy sites. The extent of avoidance of closed canopy ponds raises the question of whether those ponds are perceived as lower quality habitat, or simply not perceived as habitat at all. If closed canopy ponds are perceived as low-quality habitat, theory predicts their eventual colonization when open canopy ponds become saturated with colonists (sensu the Ideal Free Distribution), e.g., if open canopy ponds are numerically rare, or if open canopy sites have their quality reduced by factors such as predatory fish (Binckley and Resetarits 2005; Brodin et al. 2006). If they are not perceived as habitat or are not encountered because of a simple “do not enter the forest” rule, habitat availability may be considerably reduced. Clearly, more work is needed to determine the cues involved, and how finer gradients of canopy coverage (not simply endpoints) are assessed by these and other species, and how that variation affects fitness (see Rieger et al. 2004). How species partition complex spatial landscapes and how communities and

Table 1 Split-plot ANOVAs for the effect of block, canopy, nutrient addition, and the canopy \times nutrient interaction on the mean number of *Hyla squirella* and *H. chrysoscelis* eggs, *Tropisternus lateralis* egg cases, aquatic insect abundance, and aquatic insect richness

Source	df	ss	ms	F	P
<i>Hyla squirella</i>					
Block	3	5703.35	1901.11	8.24	0.0030
Canopy	1	33214.01	33214.01	144.0	<0001
Error (1)	3	5703.35	1901.11		
Nutrient	2	807.86	403.93	1.75	0.2151
Canopy \times nutrient	2	807.86	403.93	1.75	0.2151
Error (2)	12	2767.89	230.65		
Total	23	49004.34			
<i>Hyla chrysoscelis</i>					
Block	3	3047.79	1015.93	2.71	0.0916
Canopy	1	13398.61	13398.61	35.77	<0001
Error (1)	3	192.79	64.26		
Nutrient	2	259.69	129.84	0.35	0.7139
Canopy \times nutrient	2	437.64	218.82	0.58	0.5727
Error (2)	12	4495.19	374.59		
Total	23	21831.73			
<i>Tropisternus lateralis</i>					
Block	3	21.68	7.22	8.64	0.0025
Canopy	1	129.33	129.33	154.65	<0001
Error (1)	3	21.68	7.22		
Nutrient	2	15.57	7.78	9.31	0.0036
Canopy \times nutrient	2	15.57	7.78	9.31	0.0036
Error (2)	12	10.03	0.83		
Total	23	23	213.87		
<i>Abundance</i>					
Block	3	16.17	5.39	26.96	<0001
Canopy	1	205.59	205.59	1027.87	<0001
Error (1)	3	25.46	8.48		
Nutrient	2	0.48	0.24	1.21	0.3325
Canopy \times nutrient	2	0.074	0.037	0.19	0.8328
Error (2)	12	2.40	0.20		
Total	23	250.19			
<i>Species richness</i>					
Block	3	1.73	0.57	5.02	0.0175
Canopy	1	29.48	29.48	256.36	<0001
Error (1)	3	1.37	0.45		
Nutrient	2	0.12	0.06	0.52	0.6058
Canopy \times nutrient	2	0.09	0.04	0.43	0.6587
Error (2)	12	1.38	0.11		
Total	23	34.19			

Data were square-root-transformed

metacommunities are structured will depend upon whether canopy cover is perceived and responded to as a continuous variable, or there are discrete, threshold responses, as observed in response to predatory fish (Rieger et al. 2004).

Spatial and temporal variation in canopy cover can be generated seasonally, via leaf phenology, gradually via succession, or rapidly, by natural or anthropogenic disturbance (Hill et al. 2001; Rubbo and Kiesecker 2004). Aquatic systems are globally experiencing rapid change in the surrounding terrestrial landscapes, whether through widespread deforestation, or via increases in percent forest cover through suppression of natural disturbance regimes, such as fire, and conversion of abandoned agricultural land to forest (Frost 1995; Groom and Schumaker 1993; Tilman et al. 2000; Chen et al. 2006). Predicting how changes to terrestrial landscapes affect aquatic systems requires a mechanistic understanding of how species behaviorally respond to their environment. Our data suggest that habitat selection could be the primary response of many aquatic taxa to larger scale changes in forest cover, and that changes in species distribution and abundance resulting from changes in canopy cover will be produced by behavioral redistribution of adults and propagules among available habitats (Figs. 1, 2, 3).

The metacommunity-level consequences of multispecies habitat selection will depend principally on the number and spatial distribution of habitat types, the strength of the avoidance/attraction behavior these elicit, and the degree to which habitat preferences are shared by member species (Binckley and Resetarits 2005; Resetarits et al. 2005). As habitat selection involves a redistribution of individuals without necessarily involving mortality, its implications for the dynamics of populations, communities, and metacommunities are clearly distinct from mechanisms invoking differential post-colonization mortality. For example, preferred habitat patches showed increased interspecific density and species richness as habitat preferences were largely shared among species (Figs. 2, 3). This changes the intensity, frequency, and identity of particular competitive and predatory interactions exemplified here by the expected increase in intra- and interspecific competition among *Hyla* tadpoles and increased predation on these species by larval *T. lateralis*, resulting from shared preferences for open canopy/fishless ponds (Figs. 2, 3) (see Binckley and Resetarits 2003, 2005).

Habitat selection in response to a variety of both biotic and abiotic conditions is proving to be a critical factor in generating patterns of species distribution and abundance among ecological communities at multiple spatial scales (Resetarits and Wilbur 1989; Blaustein 1999; Morris 2003; Binckley and Resetarits 2005; Resetarits 2005). Processes of dispersal and colonization play a critical role in shaping communities over natural landscapes, and that realization has given rise to, among other things, the concept of the metacommunity. However, habitat selection functions quite differently from random or passive processes of dispersal and colonization. Rates of colonization are directly tied not

both to specific characteristics of communities, and to characteristics of the surrounding landscape. When multispecies habitat selection strongly connects patches of the same habitat type via shared species, or strongly connects habitats of different type via species avoidance, spatial substructure is generated within metacommunities. Thus, integrating habitat selection specifically into our consideration of community dynamics at the landscape scale, as well as into metacommunity theory, will greatly increase the generality of our approach and the utility of community and metacommunity models for predicting the dynamics of species distribution and abundance, local and regional patterns of diversity, and species responses to both natural and anthropogenic change.

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