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Patch Size as a Niche Dimension: Aquatic Insects Behaviorally Partition Enemy-Free Space across Gradients of Patch Size

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ABSTRACT: Positive correlation of species richness with area is ubiquitous in nature, but the processes driving that relationship, as well as those constraining typical patterns, remain elusive. Patch size variation is pervasive in natural systems, and it is thus critical to understand how variation in patch size, as well as its potential interaction with factors like predation and isolation, affects community assembly. We crossed patch quality (fish presence/absence) with patch size to the examine effects of quality, size, and their interaction on colonization by aquatic insects. Overall, beetles favored small, fishless patches, but individual species sorted across patch size while hemipterans aggregated into large, fishless patches, producing sorting between Coleoptera and Hemiptera. Both patch size and predation risk generated significant variation in community structure and diversity. Patch size preferences for the 14 most abundant species and preeminence of species turnover in patterns of β -diversity reinforce patch size as a driver of regional species sorting via habitat selection. Species sorting at the immigration stage plays a critical role in community assembly. Identifying patch size as a component of perceived quality establishes patch size as a critical niche dimension and alters our view of its role in assembly dynamics and the maintenance of local and regional diversity.

Keywords: community assembly, diversity, enemy-free space, habitat selection, niche, species turnover.

Introduction

Variation in the size of habitat patches is a universal property of natural systems, and increasing abundance and diversity relative to patch size (area) is a ubiquitous pattern (Arrhenius 1921; Cain 1938; MacArthur and Wilson 1967;

Connor and McCoy 1979; Rosenzweig 1995). The positive relationship between species richness and patch size is partly attributable to the role of patch size in moderating extinction rates; larger patches allow more species to maintain larger population sizes, resulting in lower stochastic and deterministic extinction rates (MacArthur and Wilson 1967). With regard to immigration, effects of patch size have been considered a consequence of larger target area; under random dispersal and colonization, larger patch size increases colonization rate (Gilpin and Diamond 1976; Connor and McCoy 1979; Lomolino 1990). Sensory biology suggests that larger habitat patches may also be more easily detected (greater cue intensity or variety; Smith 2008). Viewed through the lens of habitat selection theory, however, organisms may display active preferences for patches of different size, with patch size thus functioning as another component of patch quality (Fretwell and Lucas 1970; Rosenzweig 1981; Morris 2003). We have a ubiquitous pattern (ascending species-area curves) that may arise from a variety of processes, thus requiring an experimental approach to disentangle random from deterministic and abiotic from biotic drivers.

Larger patch size has been shown to increase immigration rates and population size in a variety of species (Sih and Baltus 1987; Franken and Hik 2004), as well as to increase equilibrium levels of species diversity (Simberloff and Wilson 1969; Bender et al. 1998). However, the effect of patch size has rarely been experimentally addressed in the larger context of habitat selection and the assembly of complex communities (but see Westby and Juliano 2017). If patch size functions as a component of perceived patch quality, thereby driving colonization decisions, we can expect wide-ranging effects on species distribution, abundances, and the assembly of natural communities across gradients of patch size. The nature of these effects depends in part on whether species have shared or complementary habitat preferences and on whether patch size preferences interact with other axes of perceived patch quality. Immigration has precedence and

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thus can preclude postimmigration effects, establish the conditions under which postimmigration sorting takes place, and/or set the trajectory of the community via priority effects (Alford and Wilbur 1985; Chase 2003; Fukami 2015). Species sorting at the immigration stage (via habitat selection on patch quality) can generate patterns typically ascribed to postimmigration processes (e.g., predation, competition, physiological tolerances; Eitam et al. 2002; Binckley and Resetarits 2005; Kraus and Vonesh 2010; Resetarits and Binckley 2013). Redistribution (preimmigration) versus postimmigration (mortality) processes can alter assembly dynamics, identity, and strength of species interactions and the extent and nature of linkages among communities (Resetarits 2005; Resetarits et al. 2005; Abrams et al. 2007; Orrock et al. 2010).

Predation risk is a critical component of patch quality that strongly affects habitat selection decisions for organisms spanning the spectrum of taxa and habitats (Brooks and Dodson 1965; Werner 1983; Lima and Dill 1990; Brown et al. 1999; Valeix et al. 2009; Silberbush and Blaustein 2011; Swain et al. 2015; Emmering et al. 2018). Organisms select habitats to minimize or eliminate spatial and temporal overlap with specific predators in the search for “enemy-free space” (Jeffries and Lawton 1984). Enemy-free space was originally defined as “ways of living that reduce or eliminate a species’ vulnerability to one or more species of natural enemies,” and it was hypothesized to be an important aspect of species’ ecologies and the assembly of natural communities (Jeffries and Lawton 1984, p. 269). We suggest that competition for enemy-free space (here defined as patches lacking particular enemies) can be intense, as such habitats are often limited both spatially and temporally. Organisms sharing enemies must use multiple mechanisms to reduce the intensity of interactions in available enemy-free space (Jeffries and Lawton 1984, 1985; Schmidt 2004; Heard et al. 2006). In freshwater systems, fishless patches are a critical form of enemy-free space and can be a limited resource at local and regional scales. Such limitation may generate high levels of both intra- and interspecific competition, as well as other interactions, among fish-intolerant species (Wilbur 1987; Wellborn et al. 1996; McPeck 2008). How colonizing species mitigate the potential for intense interactions is a critical question in understanding how the local and regional diversity of organisms in fishless or other enemy-free habitats is maintained.

Our overall goal was to link general and taxon-specific patterns of patch size-based and predation-based habitat selection to community assembly in aquatic insects. We asked whether colonizing aquatic insects preferred patches of a given size, whether those preferences were shared or variable among species and higher taxa, whether preferences were affected by predation risk, and last, how those choices translated into local and regional diversity and com-

munity structure. We used a naturally colonized experimental landscape, crossing a known component of patch quality (predation risk) with patch size (potentially a component of patch quality) to examine the specific effects of each factor and their interaction on the colonization dynamics of a diverse assemblage of aquatic insects (fig. 1).

Methods

Study Species

The University of Mississippi Field Station (UMFS) contains a diverse array of aquatic insects, including 132 recorded species of aquatic beetles (M. R. Pintar and W. J. Resetarits, unpublished data). Aquatic insects colonize natural and man-made habitats ranging from tree holes to large lakes and rivers (Batzer and Wissinger 1996; Kitching 2001), can reach high density and diversity in small patches (Matta 1973), and are primary components of aquatic communities (Wellborn et al. 1996; Wilbur 1997). Many are strong dispersers, but among taxa with aquatic adults, dispersal is energetically costly and initial colonization is critical, as secondary dispersal typically occurs only if conditions dramatically change (Zalom et al. 1979; Roff 1990; Jeffries 1994; Zera and Denno 1997; Bilton 2014). Many colonizing insects select habitats based on perceived risk (e.g., predators) and perceived reward (e.g., higher resources; Abjornsson et al. 2002; Eitam et al. 2002; Binckley and Resetarits 2005, 2009; Vonesh et al. 2009; Kraus and Vonesh 2010; Pintar and Resetarits 2017a).

Dytiscids and hydrophilids are the dominant beetles in many lentic habitats and are the most abundant beetle taxa at UMFS. Larval and adult dytiscids and larval hydrophilids are predaceous, whereas adult hydrophilids are omnivores/scavengers (Testa and Lago 1994; Larson et al. 2000). The most abundant families of aquatic Hemiptera at UMFS are Notonectidae, which are predaceous, and Corixidae, which are mostly herbivorous (Merritt et al. 2008). We might expect patch size preferences to vary by trophic level, as predators should have higher extinction rates in smaller patches, but complex life histories and trophic ambiguity, especially for the beetles, preclude simple assignment to trophic position (Schoener 1989; Holt et al. 1999).

The majority of these species are highly susceptible to predation by fish, and we used two North American fish that cover a range of gape sizes and habits as model predators to provide a more generalized fish treatment and to reduce the potential for interspecific aggression (especially in *Lepomis*) and resource competition due to high conspecific density. The green sunfish, *Lepomis cyanellus*, is one of the most widespread fish in North America, is widely introduced to previously fishless waters both inside and outside its native range (Lee et al. 1980), and is one of the most

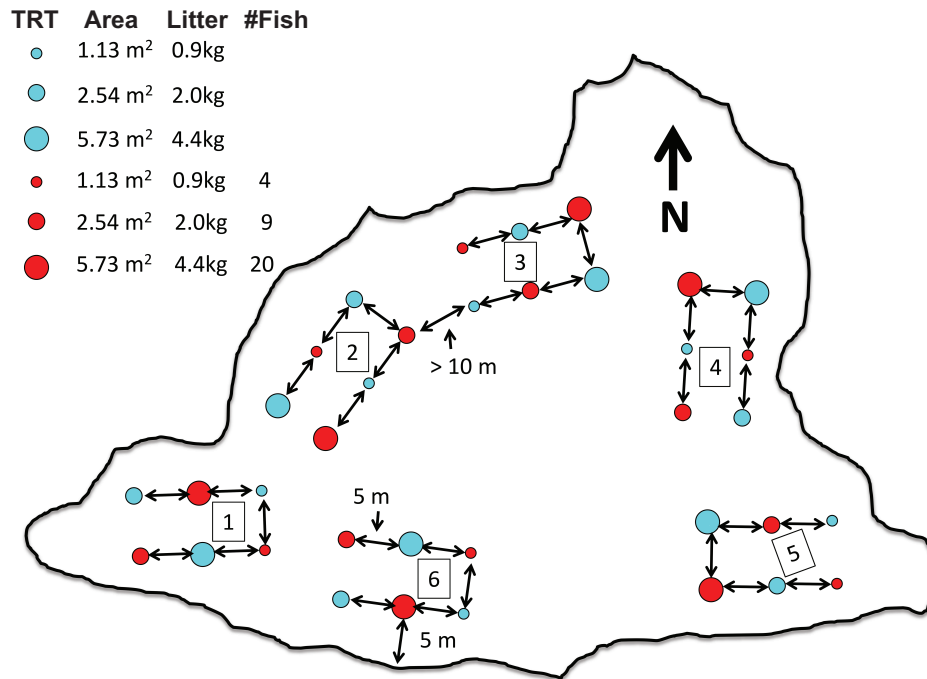


Figure 1: Schematic of experimental layout. Patch size is approximately to scale. Blue = fishless; red = fish. The enclosing line represents the edge of an old field surrounded by mixed forest.

abundant fish at UMFS. They are wide-gaped generalist predators that feed at all depth levels in ponds and strongly repel beetle colonization (Resetarits and Pintar 2016). The golden shiner, *Notemigonus crysoleucus*, is a small, pelagic, largely planktivorous, gape-limited fish that also strongly repels beetle colonization (W. J. Resetarits, J. R. Bohenek, and M. R. Pintar, unpublished data). It is widespread in North America and widely introduced as a forage fish (Lee et al. 1980).

Experimental Design

We directly and independently manipulated patch quality (fish presence) and patch size in an experiment conducted in a large old field at UMFS in Lafayette County, Mississippi. We constructed six rectangular mesocosm arrays (blocks) of six pools each ($n = 36$), completely crossing three pool sizes (1.13, 2.54, and 5.73 m²) with the presence/absence of an equal mixture of *L. cyanellus* and *N. crysoleucus* (fig. 1). Pools were of the same material, color, and shape (cylindrical), although the largest pools were 13 cm deeper, which was compensated by filling all pools to the same depth (50 cm); pools held ~525, 1,180, and 2,650 L, respectively. Treatments were randomly assigned to positions, subject to the caveats that pools of the same size were opposite one another in the two rows of each block, that each row contained alternating fish and fishless pools (fig. 1), and that an equal number

of blocks had more fish or fishless pools on the forest side. We minimized the potential for spatial contagion of risk (Resetarits and Binckley 2009) by separating pools within a block by 5 m, which was the farthest distance practical at our field site while allowing replication and preserving the patch choice aspects. Blocks were separated by >10 m between the nearest pools (fig. 1) and were identical in content, which also reduces contagion effects—there are no better choices available in terms of spatial context.

We began filling pools with well water on May 9, 2016, one block at a time, completing two blocks per day. During filling, pools were covered with tight-fitting fiberglass screen lids (1.3 mm × 1.13 mm opening) to prevent any colonization. Concurrent with filling, dried leaf litter (mixed hardwoods) was added to patches (pools) of different size in proportion to the volume (fig. 1), with all blocks completed by May 11. Fish species were held in separate holding tanks before the experiment, and we haphazardly sampled fish from these tanks (mean per-fish mass for each species = ~3.5 g). On May 11, each patch received fish at an initial density of ~2.6 g per 100 L; small patches received two *N. crysoleucus* plus two *L. cyanellus*, medium patches received four or five *N. crysoleucus* plus four or five *L. cyanellus*, and large patches received 10 *N. crysoleucus* plus 10 *L. cyanellus*. Because medium patches required an uneven number of fish, medium fish patches in blocks 1, 3, and 5 received one extra

L. cyanellus, while those in blocks 2, 4, and 6 received one extra *N. crysoleucus*. We equalized fish density, biomass, and size structure within blocks by creating eight matched pairs consisting of one large and one small individual for each species (by eye, to minimize fish stress) and randomly assigned the appropriate number of pairs to each fish patch within that block. This biomass density is on the lower end of that used in previous experiments and in natural ponds (Mittelbach et al. 1995) but above the threshold eliciting avoidance in many insects (Binckley and Resetarits 2005; Resetarits and Binckley 2009). Numerous experiments suggest that most insects do not enter the water to assess predator chemical cues (Silberbush et al. 2010; Eveland et al. 2016).

On May 12, screen lids were submerged to allow colonization and facilitate collection while preventing fish predation or harassment of colonists. Adult insects were collected and preserved weekly for quantification and identification. Very small, highly vagile species, such as *Microvelia* and surface-dwelling dipterans, could not be reliably sampled. All other taxa were exhaustively sampled and identified to species, with the exception of *Buena*, *Paracymus*, and *Sigara*, which were identified to genus. Identifications primarily used Testa and Lago (1994), Larson et al. (2000), Epler (2006), and Epler (2010). The experiment ended on July 21, after 70 days (10 weekly samples). Overall fish survival was 92% (*L. cyanellus*, 91%; *N. crysoleucus*, 93%), with no observed differences between fish species or patch sizes.

Data Analysis

We used a randomized complete block design crossing three levels of patch size (size) with two levels of predator treatment (fish). Abundance of all insects and constituent taxa were rescaled to the relative size of the smallest patches (fig. 1), and we analyzed the following three metrics related to richness: species-area relationships, species density, and rarefied species richness. Abundance is a critical measure of species preferences and is especially important for species interactions and the composition of assembled communities. We compared species-area relationships for fish and fishless patches to allow comparisons with other studies and to illustrate that the relationship is essentially linear for the size range here, as is the overall species-abundance relationship (fig. A1, available online), both of which simplify analysis of species density (Gotelli and Colwell 2011; Rosenzweig et al. 2011). Species density is a primary concern in our study and is a widely used metric (albeit often applied incorrectly) in conservation biology (Rosenzweig et al. 2011). It addresses the question of whether the number of species per unit area varies with patch size, which here speaks to the mechanisms of community assembly at work. Concep-

tually, species density should be thought of as $(\text{no. species/patch area}) = (\text{no. species/no. individuals}) \times (\text{no. individuals/patch area})$ (James and Wamer 1982; Gotelli and Colwell 2011), acknowledging the importance of abundance. Thus, we analyzed species density using abundance as a covariate, which effectively rarefies raw species density, given the essentially linear species-area and species-abundance relationships (see above). Rarefied species richness addresses the following hypothetical question: If all patches received the same number of colonists, would we see a signal of treatment on richness? For our study, this question is of interest but less important than whether species per unit area varied because, from the perspective of community assembly, the joint signal of abundance and richness is more germane, but analysis of rarefied richness again allows comparisons with other studies. Richness was rarefied for each patch using individual-based rarefaction and extrapolation in EstimateS (ver. 9.1.0; Colwell 2013), generating a unique rarefaction curve for each patch (sample). Fish patches had from 15 to 162 colonists, and fishless patches had from 74 to 708. Because 15 is so extreme, we rarefied to the next highest value, 27, and extrapolated the pool with 15 up to 27 (Colwell et al. 2012). Scaled abundance, species density, and rarefied species richness were transformed $((X + 0.5)^{1/2})$ to meet the assumptions of ANOVA (Steel et al. 1997) and analyzed using general linear mixed model ANOVA (ANCOVA for species density) in PROC MIXED (SAS Institute), with size and fish as fixed factors and block as a random factor. Block was removed from the analysis if block effects estimated as zero. The same analysis was used on α -diversity expressed as effective numbers (Jost 2007; based on Shannon diversity $(\exp(H))$) calculated using PRIMER7 (Clarke and Gorley 2015). All ANOVA-based analyses used SAS version 9.4 (SAS Institute 2016) with type III sums of squares and $\alpha = .05$.

To visualize aspects of community structure, we produced bubble plots of relative proportions based on scaled abundance for the 14 most abundant species and a shade plot (heat map of square root transformed scaled abundance) including all 58 species. We used permutational MANOVA (PERMANOVA) to test for differences in multivariate centroid location (average community composition) and permutational analysis of multivariate community dispersion (PERMDISP) to examine broad-sense β -diversity (Anderson and Walsh 2013; Anderson et al. 2015). As a measure of location, PERMANOVA is robust to variation in dispersion for balanced designs, so we can assess contributions of both multivariate location and dispersion (Anderson and Walsh 2013). This measure of β -diversity (multivariate community dispersion using PERMDISP) is not strictly independent of α -diversity but is more intuitive and relates more directly to our stated questions by capturing variation in richness, abundance, and species composition. It also allows use of

the replicated design structure to analyze β -diversity directly. Analyses of similarity used the Bray-Curtis index (abundance and species composition), and we visualized the raw data using nonmetric multidimensional scaling (NMDS). We used a second approach to decompose β -diversity into additive contributions of nestedness (β_{NES}) and species turnover (β_{SIM}) using multiple-site measures of presence/absence dissimilarity (Baselga 2010), as well as multisite Bray-Curtis decomposing (β_{BC}) into additive components due to balanced variation ($\beta_{\text{BC.BAL}}$) and abundance gradients ($\beta_{\text{BC.GRA}}$; Baselga 2017). $\beta_{\text{BC.BAL}}$ and $\beta_{\text{BC.GRA}}$ are the abundance-based analogs of turnover and nestedness, respectively (Baselga 2017). PERMANOVA, PERMDISP, NMDS plots, and shade plots used PRIMER 7 with the PERMANOVA+ add-on (Anderson et al. 2015; Clarke and Gorley 2015); bubble plots were created using SigmaPlot version 13. Partitioning of β -diversity used the beta.multi and beta.multi.abund functions in the R package beta.part (ver. 1.5.0; Baselga 2010, 2017). Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.10b64m4>; Resetarits et al. 2019).

Results

Our experiment was colonized by 6,875 insects—5,782 individuals of 51 species of aquatic beetles (Coleoptera, seven families) and 1,093 individuals of seven species of aquatic true bugs (Hemiptera, four families; table A1; tables A1–A5 are available online). Hydrophilidae (20 species) and Dytiscidae (24) were the dominant beetles, comprising 88% of total beetle species and 99% of total beetle individuals, with 86 individuals total from five other families.

Abundance

Scaled abundance for all insects was significantly affected by both patch size and fish and was highest in small, fishless patches (table 1; fig. 2a). Hydrophilids and dytiscids both had significantly higher scaled abundance in small, fishless patches (table 1; fig. 2b, 2c). Hemipterans showed significant responses to both patch size and fish, and scaled abundance was highest in large, fishless patches (table 1; fig. 2d).

Table 1: Fixed effects results (type III) from mixed model ANCOVA on species density (abundance as covariate; fig. 4b), and ANOVAs on rarefied species richness of all insects (fig. 4c) and abundance of individual taxonomic groups (fig. 2a–2d)

Source	df _N	df _D	F	P
Species density:				
Abundance	1	29	14.81	.0006
Size	2	29	74.53	<.0001
Fish	1	29	1.55	.2235
Size × fish	2	29	6.56	.0045
Rarefied species richness:				
Size	2	25	13.96	<.0001
Fish	1	25	.26	.6122
Size × fish	2	25	1.45	.2546
Abundance:				
All insects:				
Size	2	25	15.01	<.0001
Fish	1	25	69.49	<.0001
Size × fish	2	25	.1	.9027
Hydrophilids:				
Size	2	25	4.58	.0202
Fish	1	25	26.41	<.0001
Size × fish	2	25	.37	.692
Dytiscids:				
Size	2	25	34.8	<.0001
Fish	1	25	66.67	<.0001
Size × fish	2	25	1.55	.2326
Hemipterans:				
Size	2	25	45.4	<.0001
Fish	1	25	30.74	<.0001
Size × fish	2	25	13.79	<.0001

Note: Boldfacing indicates significance. Different degrees of freedom for species density reflect removal of zero estimated block effect from the model. See table A1 and figure 3a for individual species results.

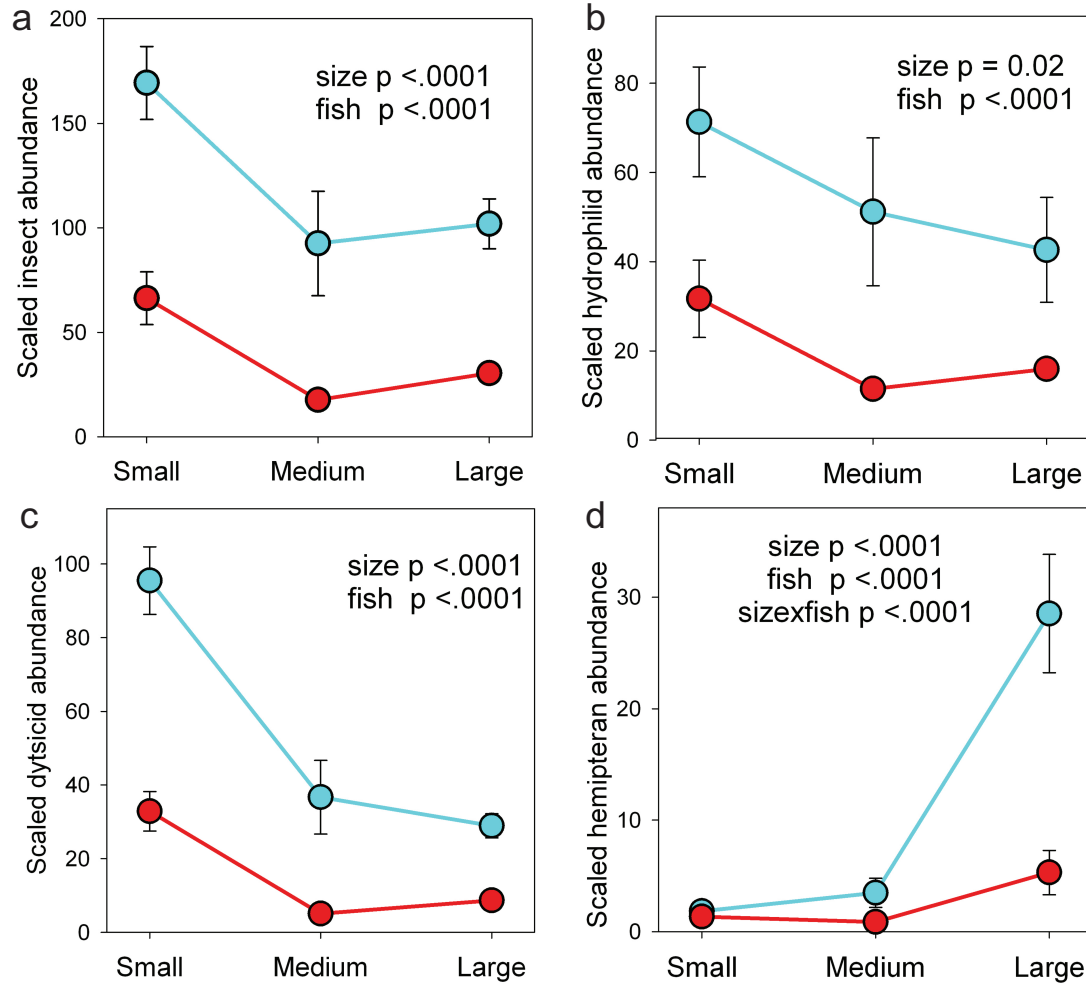


Figure 2: Responses of colonizing organisms of different taxa to fish presence/absence and patch size for abundance (mean \pm 1 SE) scaled to the size of the smallest patch for all insects (a), hydrophilids (b), dytiscids (c), and hemipterans (d). Blue = fishless; red = fish. The X-axis scale is not linear.

The significant size \times fish interaction reflected large variation among sizes in fishless patches but not in fish patches.

Six of the 10 most abundant beetles (*Copelatus glyphicus*, *Paracymus*, *Enochrus ochraceus*, *Berosus infuscatus*, *Tropisternus lateralis*, and *Laccophilus fasciatus*) significantly preferred fishless patches; *L. proximus* had a marginal preference for fishless patches; and only one species (*Cymbiodyta chamberlaini*) was more abundant in fish patches, but this was not significant (table A1; fig. 3a). Four of the 10 most abundant species (*C. glyphicus*, *Paracymus*, *E. ochraceus*, and *C. chamberlaini*) significantly preferred small patches, while three preferred large patches (*Tropisternus collaris*, *T. blatchleyi*, and *Laccophilus proximus*) and one had a marginally nonsignificant preference for large patches (*T. lateralis*; table A1; fig. 3a). Significant size \times fish interactions were due to preferences for size manifesting only in fishless patches, fish patches being uniformly avoided (table A1;

fig. 3a). The four most abundant hemipterans (*Notonecta irrorata*, *Hesperocorixa vulgaris*, *Buenoa*, and *Sigara*) significantly preferred large, fishless patches (marginal fish effect, *N. irrorata*), and significant interactions were as described above (table A1; fig. 3a).

Assemblage Structure and Diversity

In total, 5,324 individuals of 57 (of 58 total) species colonized fishless patches (98%), versus 1,551 of 40 species for fish patches (69%). Small, medium, and large patches received a cumulative total of 37 (64%), 43 (74%), and 55 (91%) species, respectively (fig. 3b). Species-area plots for fish and fishless patches (raw data) show expected patterns of increasing richness with size. Slopes are marginally nonsignificantly different but with significantly different intercepts (fig. 4a).

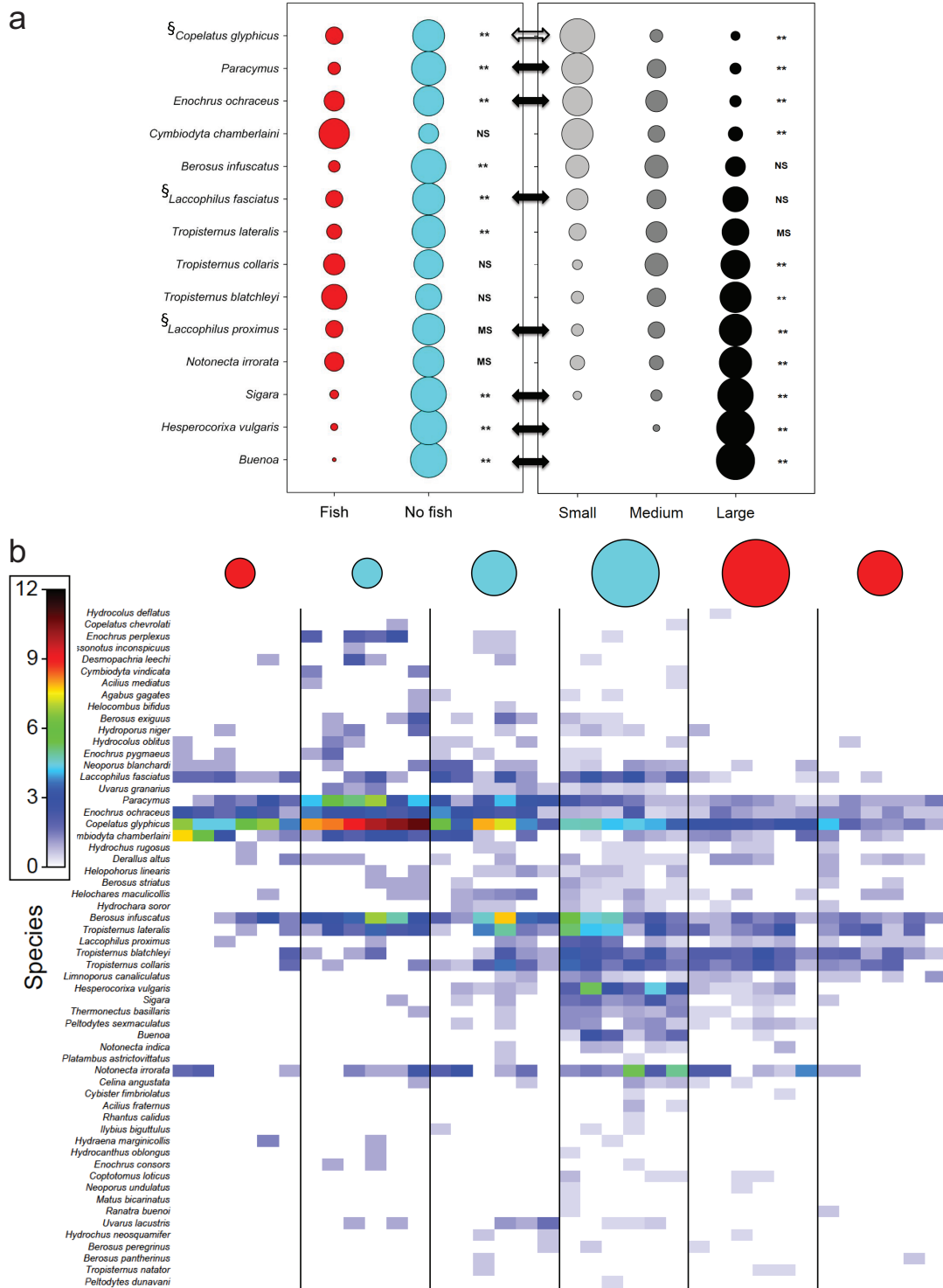


Figure 3: a, Bubble plot of proportion of each species in fish versus fishless patches (left) and patches of different size (right) for the 14 most abundant species (≥ 72 individuals total). Data are from an ANOVA on transformed $(X + 0.5)^{1/2}$ abundances using Fisher's protected least significant difference test. The left panel shows the main effect of fish; the right panel shows the main effect of size. Significance is as follows: two asterisks indicate $P < .01$, MS indicates $.05 < P < .1$, and NS indicates $P > .1$ (ANOVA details are in table A2). Solid arrows indicate a significant fish \times size interaction ($P < .05$); the open arrow indicates marginal interaction ($.05 < P < 0.1$). The top 10 species are Coleoptera, those with a section sign (§) are Dytiscidae, others are Hydrophilidae, and the bottom four are Hemiptera. Species ordered by abundance within order. b, Shade plot (heat map) showing square root transformed abundances for the entire insect assemblage. Warmer colors indicate greater abundance. Treatment symbols: red = fish; blue = fishless; circle size indicates patch size. Treatments are ordered by similarity, and species order is based on similarity of distribution (see table 2; fig. 6).

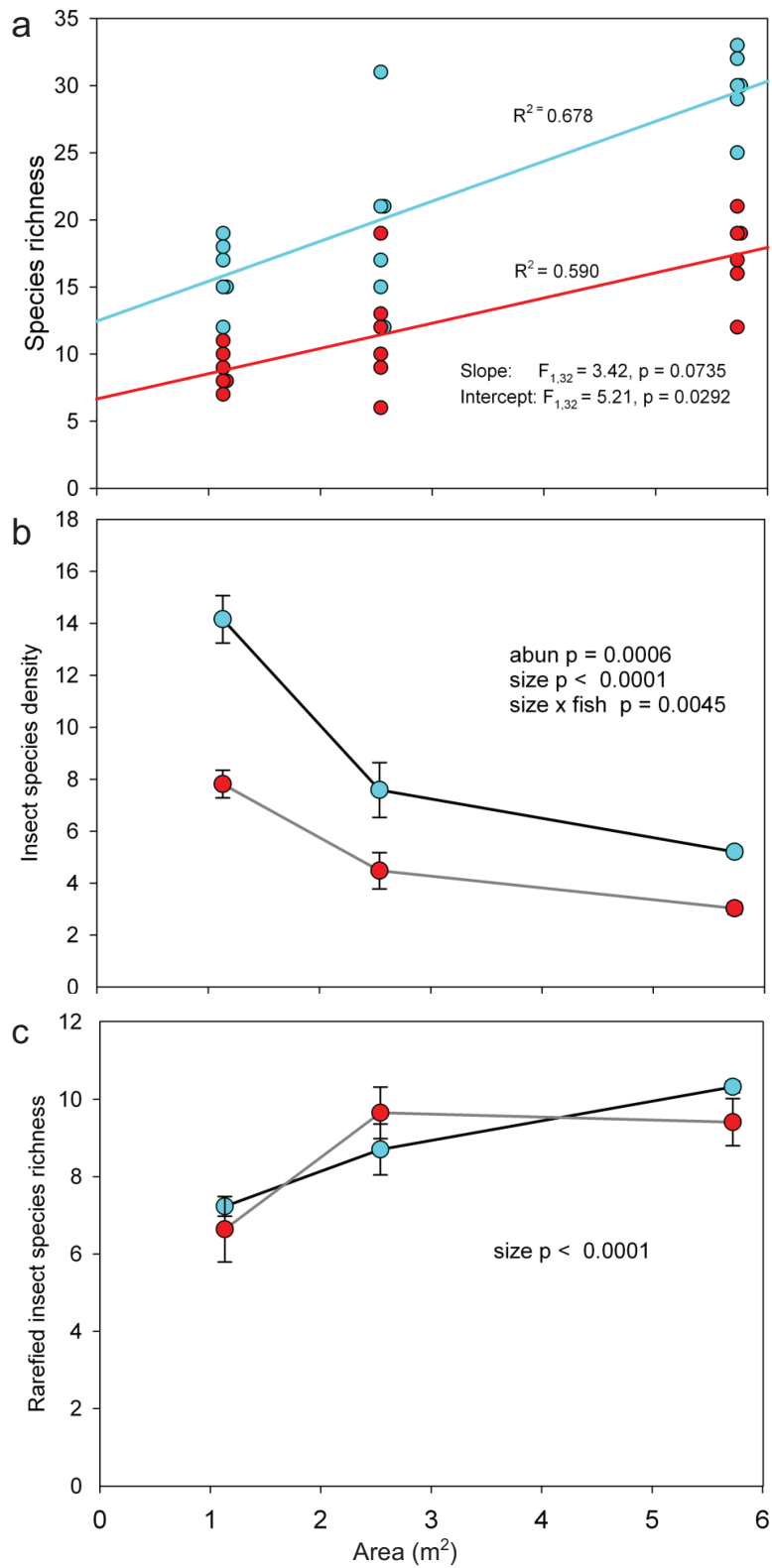


Figure 4: *a*, Insect species-area relationships and best fit regression lines plotting raw species richness versus patch size for fish and fishless patches. *b*, Uncorrected insect species density (mean \pm 1 SE; species per unit area; see “Methods”) showing results of ANCOVA with abundance as the covariate. Size has an effect independent of abundance, whereas fish effect is driven by variation in abundance. *c*, ANOVA results for rarefied insect species richness (mean \pm 1 SE; see “Methods”). Note the relative flatness of species-area relationships in *a* and *c* (see “Discussion”). Red = fish patches; blue = fishless patches.

Species density was significantly affected by abundance, size, and the size \times fish interaction, with highest species density in small patches. Size explained the largest proportion of variation independent of abundance (table 1; fig. 4*b*), while fish effects on species density were driven by abundance (table 1; fig. 4*b*). Size, but not fish, had a significant effect on rarefied species richness (table 1; fig. 4*c*). Richness showed the expected increase with area, but the flatness of accumulation curves for both raw (fig. 4*a*) and rarefied (fig. 4*c*) richness support the idea that preference for small patches, rather than saturation of the species-abundance relationship in larger patches, is the critical factor. This is borne out by the rarefaction curve for the entire data set (fig. A1), which indicates that all patch totals fall on the steeply ascending and largely linear portion of the curve.

Beetles largely aggregated into fishless patches and sorted across the patch size gradient, while hemipterans aggregated with regard to both size and fish (fig. 3*a*). Figure 3*b* illustrates sorting across treatments for the entire insect assemblage. Mean α -diversity was significantly affected by size alone for all insects; by size, fish, and size \times fish interaction for dytiscids; and by size and a marginal size \times fish interaction for hydrophilids and hemipterans (table A3; fig. 5). For fishless patches, all groups except hydrophilids show the pattern expected based on raw species richness, with α -diversity increasing with patch size.

NMDS plots (fig. 6) visualize the differences among treatments formally analyzed with PERMANOVA and PERMDISP (tables 2, A4). Interactions are undefined for PERMDISP; thus, each main effect was analyzed separately (mean and SE in table A4 for the crossed treatments).

For all insects, hydrophilids, and dytiscids, both multivariate location (average community composition) and multivariate dispersion (β -diversity as community dispersion) were significantly different (tables 2, A4; figs. 5*b*, 6). Differences were driven by size, fish, and the interaction (marginal for hydrophilids) for location and by size alone for dispersion, with medium patches typically showing the greatest dispersion (highest β -diversity), especially in fishless patches (table A4; figs. 5*b*, 6). For hemipterans, location was significant for size, fish, and the interaction and dispersion was significantly different for size only (tables 2, A4; figs. 5*b*, 6), but results should be viewed with caution due to an unbalanced design resulting from missing cells (Anderson and Walsh 2013).

Variation in β -diversity strongly reflects species turnover rather than nestedness for both presence/absence (Sorensen) and abundance-based (Bray-Curtis) measures (fig. 7; table A5). Partitioning was similar for presence/absence and abundance data for all insects, beetles, and hydrophilids. For all insects, using presence/absence, species turnover explained 89%, 83%, and 86% of β -diversity for the full design, fish patches, and fishless patches, respectively. For

abundance-based measures, turnover accounted for 85%, 83%, and 78% of β -diversity for the full design, fish patches, and fishless patches, respectively. The only exceptions were the less species-rich hemipterans, which showed a predominant contribution of nestedness (68%) for presence/absence data in fishless patches, while dytiscids showed higher nestedness (54%) for abundance-based β -diversity in fishless patches.

Discussion

Differential rates of immigration and extinction, in conjunction with mechanisms of local and regional species coexistence, are key factors determining biological diversity at the community (local) and metacommunity (regional) scale (MacArthur and Wilson 1967; Hanski 1999; Chase and Leibold 2003; Leibold et al. 2004). Species turnover is ubiquitous in natural systems, and factors affecting turnover determine how species sort and assemble into communities across time and space. The niche concept remains central to ecological theory and interest has undergone a resurgence with a more comprehensive view of a species' niche, returning to and expanding on Hutchinson's concept of the n -dimensional hypervolume (Hutchinson 1957; Chase and Leibold 2003; Colwell and Rangel 2009; Holt 2009; Fukami 2015; Godsoe et al. 2017; Letten et al. 2017; Sexton et al. 2017; Godoy et al. 2018). A key to understanding the role of the niche hinges on the actual resource axes (writ large) across which species sort in natural systems.

Studies of habitat selection in naturally colonizing organisms provide a unique window into the fundamental niche; we essentially reveal organisms' own perception of the available niche space based on their assessment of expected fitness. These perceptions, driven and fine-tuned by natural selection on sensory capabilities and behavioral algorithms, should map onto realized fitness (Rieger et al. 2004). There are limitations, however, as organisms seldom have ideal knowledge and/or the freedom to use it (Fretwell and Lucas 1970) and are susceptible to ecological traps (Delibes et al. 2001*a*, 2001*b*). Nonetheless, colonization decisions inform us about the perceived quality of habitat patches and reveal axes of multidimensional niche space that might otherwise remain obscure. Beyond community assembly, modeling suggests that habitat selection has greater adaptive potential than either adaptive plasticity or divergent natural selection (Nicolaus and Edelaar 2018).

Habitat Selection and Species Sorting

Responses of our 14 most abundant taxa reinforce the role of species turnover and the importance of patch size in species sorting (fig. 3). Beetles, including both dominant families, generally favored fishless patches but sorted across a

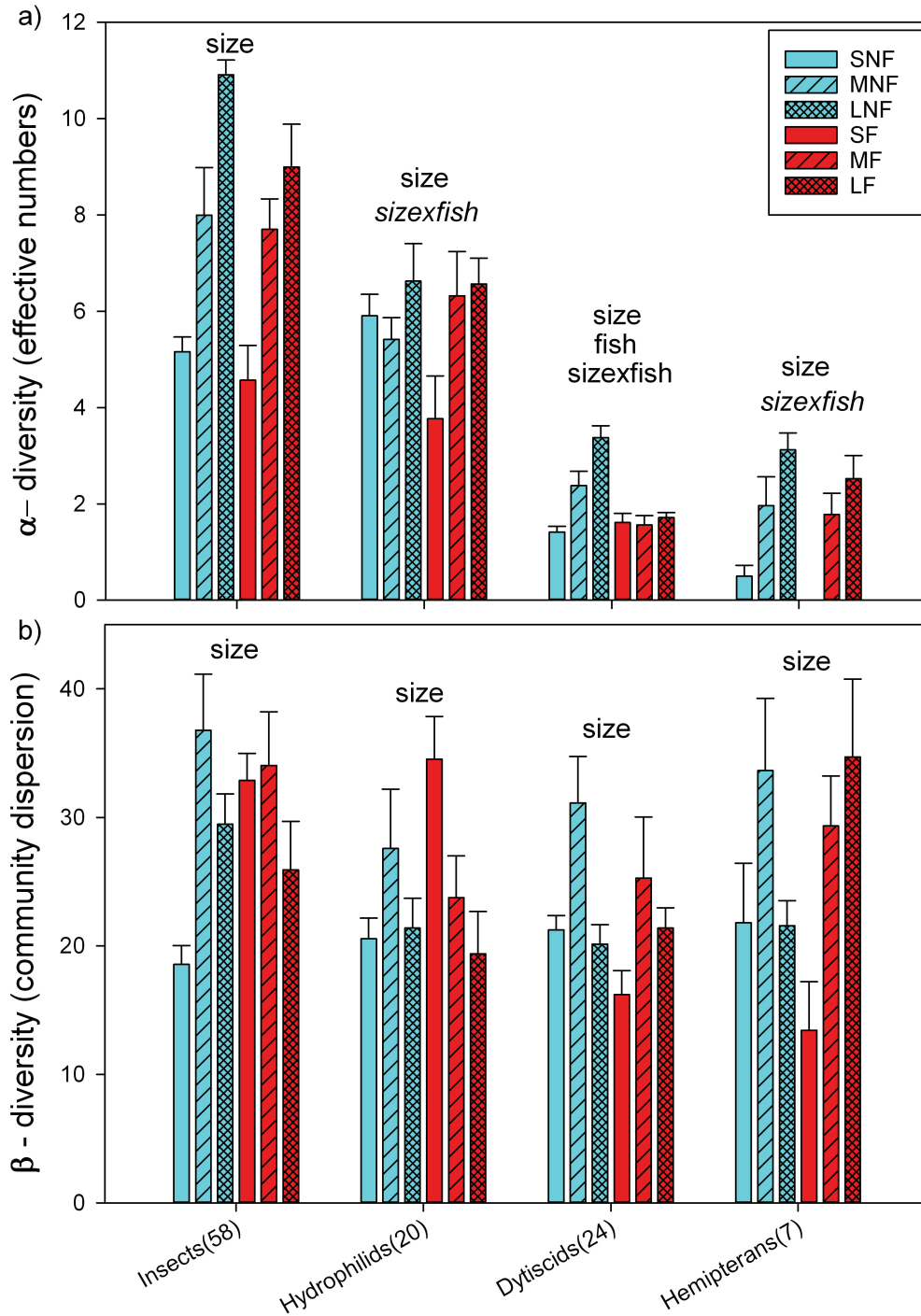


Figure 5: α -Diversity (a; mean \pm 1 SE) and β -diversity (b; mean \pm 1 SE; see fig. 6 for nonmetric multidimensional scaling plots) by treatment for the four taxonomic groups. Numbers in parentheses indicate number of species. Factors above bars are statistically significant; those in italics are marginally nonsignificant. See tables 2, A3, and A4 for detailed statistics. SNF = small, no fish; MNF = medium, no fish; LNF = large, no fish; SF = small, fish; MF = medium, fish; LF = large, fish.

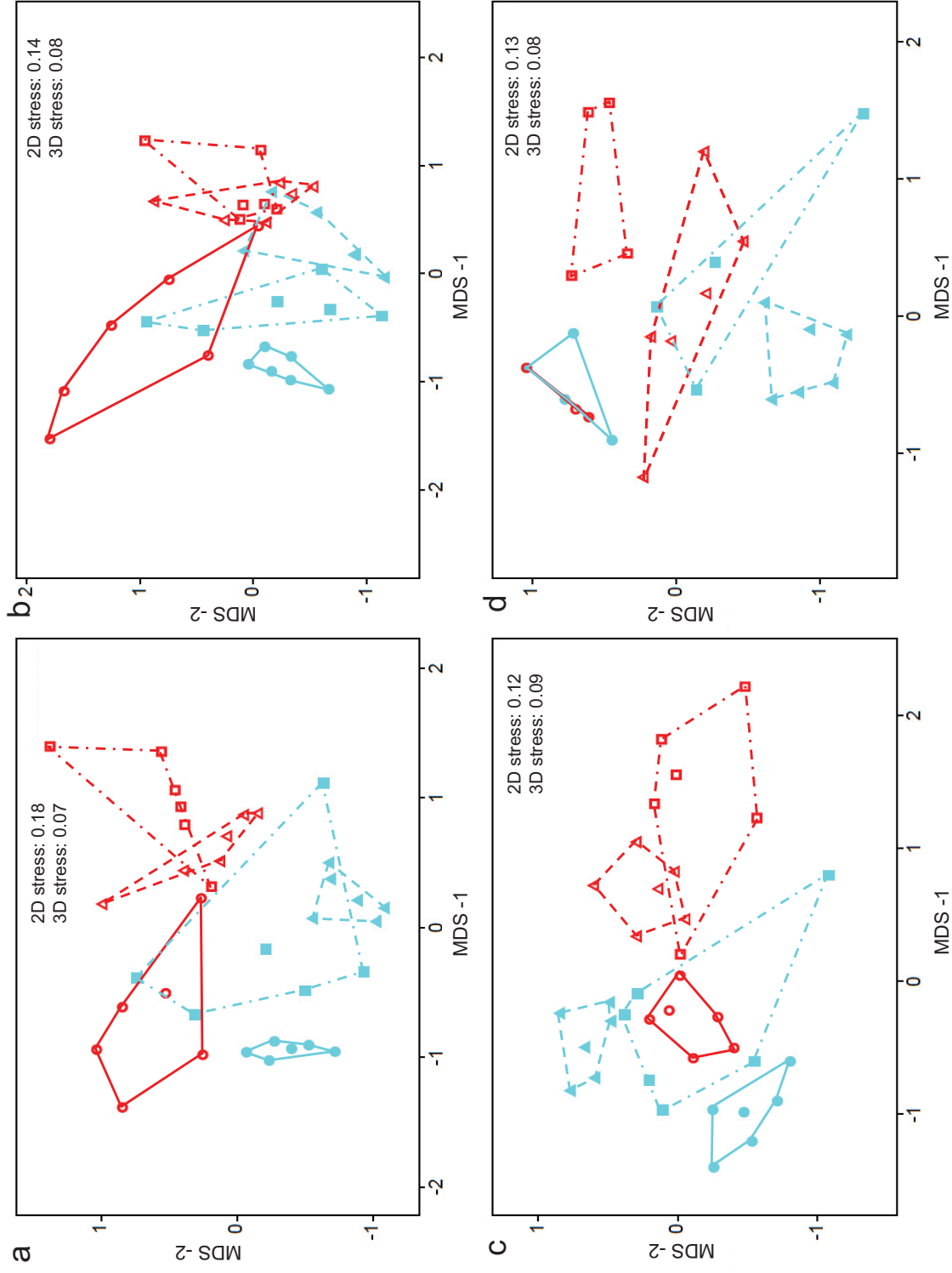


Figure 6: Nonmetric multidimensional scaling plots visualizing assemblages by size/fish treatment combinations; all insects (a), hydrophilids (b), dytiscids (c), and hemipterans (d). Circles, solid line = small; squares, dot-dash = medium; triangles, dash = large; open red = fish; closed blue = fishless. Note both the lack of overlap between fish and fishless patches for all patch sizes and the distinct lack of overlap between small and large patches across all groups. For permutational ANOVA and permutational analysis of multivariate community dispersion statistics, see tables 2 (main effects) and A4 (pairwise comparisons and treatment dispersion means).

Table 2: Permutational ANOVA (PERMANOVA) results for multivariate location (average community composition) and permutational analysis of multivariate community dispersion (PERMDISP) results for multivariate dispersion (broad-sense β -diversity) for size and fish treatments analyzed separately (figs. 5b, 6)

Source	df	SS	MS	Pseudo <i>F</i>	<i>P</i>
A. All insects (<i>S</i> = 58, <i>n</i> = 6,875):					
PERMANOVA:					
Size	2	13,850	6,924.9	8.55	.001
Fish	1	8,997.1	8,997.1	11.11	.001
Size × fish	2	5,035.8	2,517.9	3.11	.001
Res	30	24,304	810.12		
Total	35	52,186			
PERMDISP:					
Size				<i>F</i> _{1,33} = 4.836, <i>P</i> = .018	
Fish				<i>F</i> _{1,34} = .349, <i>P</i> = .602	
B. Hydrophilids (<i>S</i> = 20, <i>n</i> = 3,236):					
PERMANOVA:					
Size	2	11,685	5,842.5	7.16	.001
Fish	1	7,505.3	7,505.3	9.19	.001
Size × fish	2	2,806.1	1,403.1	1.72	.074
Res	30	24,492	816.39		
Total	35	46,488			
PERMDISP:					
Size				<i>F</i> _{2,33} = 4.814, <i>P</i> = .027	
Fish				<i>F</i> _{1,34} = .678, <i>P</i> = .475	
C. Dytiscids (<i>S</i> = 24, <i>n</i> = 2,460):					
PERMANOVA:					
Size	2	12,787	6,393.3	9.37	.001
Fish	1	11,307	11,307	16.57	.001
Size × fish	2	6,717.2	3,358.6	4.92	.001
Res	30	20,468	682.28		
Total	35	51,279			
PERMDISP:					
Size				<i>F</i> _{2,33} = 15.156, <i>P</i> = .001	
Fish				<i>F</i> _{1,34} = .1037, <i>P</i> = .774	
D. Hemipterans (<i>S</i> = 7, <i>n</i> = 1,093):					
PERMANOVA:					
Size	2	19,193	9,596.6	8.94	.001
Fish	1	4,904.5	4,904.5	4.57	.003
Size × fish	2	7,650.3	3,825.2	3.56	.003
Res	21	22,550	1,073.8		
Total	26	55,396			
PERMDISP:					
Size				<i>F</i> _{2,24} = 7.201, <i>P</i> = .013	
Fish				<i>F</i> _{1,25} = .004, <i>P</i> = .942	

Note: All *P* values are based on data permutations. Boldfacing indicates significant effects; italics indicate marginally nonsignificant effects. PERMDISP results for Hemiptera should be viewed cautiously because of missing values (due to patches with no Hemiptera) creating an unbalanced design.

gradient of patch sizes. Hemipterans strongly preferred fishless patches and, in contrast with beetles, uniformly preferred large patches. So, in aggregate, beetles preferentially colonize small patches, while hemipterans (both herbivorous and predacious taxa) prefer large patches, resulting in sorting between the taxa (fig. 2). Thus, our critical finding is that after sorting between fish and fishless patches (fig. 3a,

left), species segregated with respect to patch size (fig. 3a, right). Abundances for all 58 species (fig. 3b) further illustrate behavioral sorting across predation risk and patch size.

Despite the overall preference among beetles for small patches and the higher species density, we do see the expected pattern of an increase in species richness with area

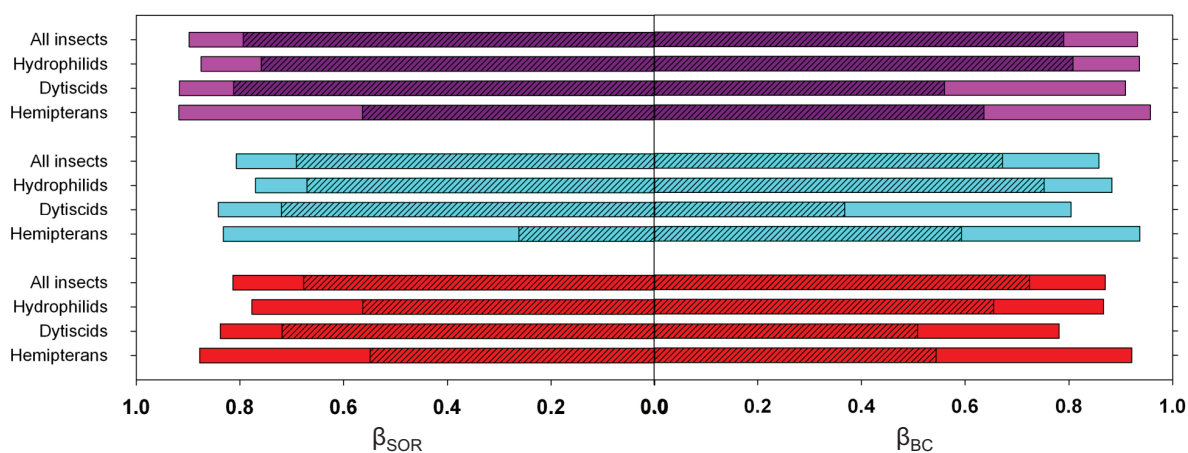


Figure 7: *Left*, total multisite β -diversity based on presence/absence data (Sorensen; β_{SOR}) partitioned between additive components attributable to species turnover (β_{SIM} = hatched) and nestedness (β_{NES} = solid). *Right*, total β -diversity based on abundance data (Bray-Curtis; β_{BC}) partitioned between additive components attributable to balanced variation ($\beta_{\text{BC,BAL}}$ = hatched) and abundance gradients ($\beta_{\text{BC,GRA}}$ = solid). $\beta_{\text{BC,BAL}}$ and $\beta_{\text{BC,GRA}}$ are the abundance-based analogs of turnover and nestedness, respectively. Data are displayed for the full design (purple), with variation due to both fish treatments and patch size, and for fishless (blue) and fish (red) treatments. β -diversity did not differ between fish and fishless treatments for any group; thus, the partitioning of diversity reflects variation due to patch size. See table A5 for detailed statistics.

(fig. 4a, 4b). However, the slopes for both raw and rarefied richness are much shallower than expected based on the increase in area; raw species richness increases by a factor of ~ 2 across a more than fivefold increase in patch area, and rarefied richness increases by even less. This can only be partly ascribed to saturation of the local species pool, as even the patch with the highest abundance (large, fishless) falls on the steeply ascending portion of the species accumulation curve (fig. A1). Since patches do not vary in habitat complexity and there is no extinction, shallow positive slopes support both a passive positive effect of size, sensu the target-area hypothesis (Gilpin and Diamond 1976; Connor and McCoy 1979; Lomolino 1990), and strong active preferences for different patch sizes that favors small patches overall (fig. 2). Ryberg and Chase (2007) showed that extinction rates per unit area have different slopes based on predation regime. Resetarits and Binckley (2013) expanded on that theme and showed that habitat selection based on perceived predation risk also depressed immigration rates. Here we see an increase in species richness with area but also clear differences in magnitude and possibly slope driven by perceived predation risk (fig. 4).

Within two genera, *Laccophilus* (Dytiscidae) and *Tropisternus* (Hydrophilidae), species show contrasting patterns of sorting across size and predation risk (fig. 3a). Both *Laccophilus* strongly avoid fish, but *L. proximus* prefers large patches, while *L. fasciatus* shows no size preference. In contrast, all three *Tropisternus* prefer large patches but vary in their response to fish, from strong avoidance (*T. lateralis*) to no preference (*T. blatchleyi*). Thus, there is sorting across

patch size and perceived predation risk between orders, among species of Coleoptera, and within genera in both beetle families (fig. 3a).

Species show different colonization strategies with respect to fish and patch size; however, there are multiple types of predators in a landscape, and avoidance is accomplished in different ways. Predator cues can be assessed directly, or risk assessment may involve patch characteristics that covary with predation risk, such as patch size or patch age (Woodward 1983; Schneider and Frost 1996; Spencer et al. 1999). *Copelatus glyphicus* avoid fish directly by strongly avoiding fish patches (Resetarits and Binckley 2009; Resetarits and Pintar 2016; this article) but may avoid other labile predators whose arrival is unpredictable (e.g., *N. irrorata*; M. R. Pintar and W. J. Resetarits, unpublished data), as well as other large insect predators, by choosing smaller patches (Spencer et al. 1999). Even our largest mesocosms (5.73 m²) rarely attract the largest insect predators, such as beetles of the genera *Cybister* and *Dytiscus* or hemipterans such as *Lethocerus* and *Belostoma*, indicating that insect size preferences extend beyond the range employed here and suggesting that patch size may serve as a surrogate for predation risk from larger insect predators.

Habitat Selection, Assemblage Structure, and Diversity

Fish have been previously shown to dramatically affect colonization in this assemblage of insects (Resetarits and Pintar 2016). Fish and fishless patches differed in scaled

abundance, taxon-specific scaled abundance, species density (table 1; figs. 2–4), and assemblage structure (tables 2, A4; fig. 6), although the effect on species density was driven by differences in abundance. Surprisingly, α -diversity differed between fish and fishless patches only for dytiscids, although there are interactions or marginal interactions with patch size for hydrophilids, dytiscids, and hemipterans (table A3; fig. 5a). Also surprisingly, neither rarefied richness nor β -diversity differed between fish and fishless patches (table 2; fig. 5b), and this held whether β -diversity was analyzed as multivariate dispersion or effective numbers (not shown). Previous work looking at combined pre- and post-colonization effects (Chase et al. 2009; Van Allen et al. 2017) found that fish decreased spatial β -diversity. The contrast with our experiment, in which fish had no effect on β -diversity, suggests that the strong deterministic effect of fish is manifested at the postcolonization stage and that colonization of fish patches is more stochastic. We suggest that colonization with respect to fish for nonavoiding species is haphazard, while the colonization of fish patches by avoiding species is largely the result of recognition or reaction errors—mistakes. The differing dynamics of pre- versus post-colonization sorting warrants further attention.

However, most unexpected were the significant and counter-intuitive differences in colonization in response to patch size itself; all of our response variables, from scaled abundance to assemblage structure, showed significant effects of patch size per se. Interestingly, medium patches generally had the highest β -diversity, especially in fishless patches, despite the fact that none of our abundant species preferred medium patches, suggesting that the greater β -diversity resulted from spillover of species with preferences for either large or small patches. All taxa with strong preferences for either large or small patches had greater abundance in the more similar patch size (medium) than in the opposite patch size (fig. 3a, right). Raw and rarefied species richness increased with patch size (fig. 4a, 4c), but communities in smaller, less species-rich patches are not simply a subset of those in larger patches, as would be expected based on passive capture alone (fig. 7; table A5). Nestedness, in the context of dispersal and colonization, implies that variation in diversity is a function of random colonization, whereas species turnover suggests nonrandom colonization, in this case, habitat selection. One clear message is that higher overall regional diversity would result from landscape-level variation in patch size; any mixture of patch sizes from our experiment would produce higher β - and γ -diversity than patches of uniform size (figs. 3, 5, 6). This has implications for conservation and restoration, especially given the debate over the relative importance of patch quantity versus quality (Mortelliti et al. 2010; Hodgson et al. 2011).

Larger patch size may positively affect colonization rate via passive capture (Gilpin and Diamond 1976; Connor

and McCoy 1979; Buckley and Knedlhans 1986; Lomolino 1990) or sensory bias (Smith 2008). We define size preference as disproportionate colonization with respect to patch size, and the fact that both large and small patches are preferred by different species contraindicates simple capture probabilities or detectability. Observed variation is not explained by organism size assortment but reflects true variation in preferences. Patch size functions as a component of patch quality and potentially interacts with other determinants of patch quality, such as predation risk, canopy cover, resource level, and substrate type, to determine species-specific colonization rates and community structure. Patch size itself thus becomes a niche dimension across which species may behaviorally sort and functions as a primary driver of community assembly. Because of strong shared avoidance of fish among many taxa, patch size may be a critical factor in species sorting and processes of community assembly in freshwater habitats, where fishless patches (enemy-free space) may be a limiting resource (Wilbur 1987; Wellborn et al. 1996; McPeck 2008). Fish-intolerant species behaviorally sort along gradients of patch size in fishless ponds, resulting in reduced levels of local competition and predation. Variation in β -diversity across patch size is dominated by species turnover in both fish and fishless patches, reinforcing the importance of habitat selection in driving community assembly and patterns of community structure.

The dynamics of perceived patch quality and how other determinants of quality interact with size have a variety of ramifications for how communities are assembled and linked into larger metacommunities (Resetarits 2005). The driving forces behind the variation in response to patch size are myriad and include both abiotic and biotic factors. We removed insects weekly, so it is unlikely that species were responding directly to each other or to community assembly (M. L. Pintar and W. J. Resetarits, unpublished data). Preference variation likely results from species-specific variation in behavioral decision-making algorithms with respect to patch size. Factors known to affect perceived patch quality in aquatic insects include fish, community assembly, canopy cover, nutrients/primary productivity, spatial context, leaf litter type, and zooplankton abundance, none of which should vary with size in our experiment or are controlled (e.g., nutrients, community assembly; Binckley and Resetarits 2005, 2007, 2008, 2009; Resetarits and Binckley 2009, 2014; Vonesh et al. 2009; Kraus and Vonesh 2010; Deans and Chalcraft 2016; Pintar and Resetarits 2017a, 2017b, 2017c). Factors varying with size in natural aquatic systems include temperature, desiccation risk, predators, resource availability, habitat heterogeneity, and a host of other characteristics. The key finding here is that patch size itself independently generates substantial variation in colonization rate and resulting species density, richness, composition, relative abundance, and both α - and β -diversity.

Colonizing insects potentially reduce the intensity of interspecific interactions, especially in fishless patches, by behaviorally sorting across gradients of patch size, facilitating increased β - and γ -diversity by decreasing the intensity of local competitive and predatory interactions. Habitat selection generates species sorting at the immigration stage that plays a preeminent role in community assembly (Binckley and Resetarits 2005; Vonesh et al. 2009; Kraus and Vonesh 2010; Resetarits and Pintar 2016), preceding and possibly preempting postcolonization processes. Variation in patch size, whether of host plants for phytophagous insects, prairie remnants for grassland birds, ponds for aquatic insects, or actual islands, is a universal characteristic of habitat patches (MacArthur and Wilson 1967), and active habitat selection occurs in mobile organisms across all animal taxa. Species sorting across gradients of patch size is of critical importance in understanding the process of community assembly, the maintenance of landscape level diversity, and the dynamics of species interactions in complex metacommunities. Local and regional coexistence explain patterns of diversity at community and metacommunity scales, and processes of species sorting can increase the potential for stable regional coexistence and transient local coexistence via source-sink dynamics. Establishing patch size as a niche dimension changes how we view the role of patch size variation in supporting local and regional diversity, as well as the importance of preserving variation in patch size as a driver of diversity.

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Many dytiscid beetles like *Thermonectus nigrofasciatus* (left) prefer smaller habitats, while aquatic true bugs like *Notonecta irrorata* (right) prefer larger habitats, spatially sorting species into different habitats based on patch size. Photo credit: Matthew R. Pinar.