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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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THIS IS THE FINAL ACCEPTED VERSION

Dear Dr. Resetarits:

The Editorial Board of The American Naturalist is pleased to inform you that your article, "Patch size as a niche dimension: aquatic insects behaviorally partition enemy-free space across gradients of patch size," has been accepted for publication. We believe your paper is now an excellent contribution that we are proud to publish. I hope you have found the review process helpful (if not, please let me know!).

There are some steps to complete before your manuscript can go to Production. I have pasted the instructions below. Thank you again for submitting your work to The American Naturalist. We look forward to seeing it in print soon.

Sincerely,

Daniel I. Bolnick
Editor-in-Chief
The American Naturalist
Professor, Department of Ecology and Evolutionary Biology, University of Connecticut

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Associate Editor Dr. Volker H. W. Rudolf 's Recommendation
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Thanks for addressing the few remaining issues, it's all clear now.

Patch size as a niche dimension: aquatic insects behaviorally partition enemy-free space

across gradients of patch size

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KEYWORDS: community assembly, diversity, enemy-free space, habitat selection, niche, species

turnover

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Article

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Supplemental figure S1.

Supplemental tables S1-S5.

The authors wish to be identified to the reviewers.

ABSTRACT: Positive correlation of species richness with area is ubiquitous in nature, but the processes driving that relationship, and those constraining typical patterns, remain elusive. Patch size variation is pervasive in natural systems, and thus it is critical to understand how variation in patch size, as well as its potential interaction with factors like predation and isolation, affect community assembly. We crossed patch quality (fish presence/absence) with patch size to 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 size and predation risk generated significant variation in community structure and diversity. Patch size preferences for the 14 most abundant species, and pre-eminence of species turnover in patterns of beta-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.

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*a*). 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, 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 increasing equilibrium levels of species diversity (Simberloff and Wilson 1969; Bender et al. 1998). However, the impact 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, thus can preclude post-immigration effects, establish the conditions under which post-immigration 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 post-immigration processes (e.g., predation, competition, physiological tolerances) (Eitam et al. 2002; Binckley and Resetarits 2005; Kraus and Vonesh 2010; Resetarits and Binckley 2013). Redistribution (pre-immigration) vs post-immigration (mortality) processes can alter assembly dynamics, identity and strength of species interactions, and 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 impacts 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 hypothesized to be an import aspect of species' ecologies and the assembly of natural communities (Jeffries and Lawton 1984). 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 utilize 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; McPeek 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- 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 lastly, how those choices translated into local and regional diversity and community 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 123 recorded species of aquatic beetles (Pintar and Resetarits, unpubl. data). Aquatic insects colonize natural and man-made habitats ranging from treeholes 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 2017*a*).

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, precludes 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 fishes 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 fishes in North America, is widely introduced to previously fishless waters both inside and outside of its native range (Lee et al. 1980), and is one of the most 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 (unpubl. 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 6 rectangular mesocosm arrays (blocks) of 6 pools each (N=36), completely crossing

3 pool sizes (1.13 m^2, 2.54 m^2 and 5.73 m^2) 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), though the largest pools were 13cm deeper, which was compensated by filling all

pools to the same depth (50 cm); pools held ~593, 1334, and 3002 L respectively. Treatments

were randomly assigned to positions, subject to the caveat 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 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 meters, which was the furthest distance practical at

our field site while allowing replication and preserving the patch choice aspects. Blocks were

separated by >10 m between 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 9 May 2016, one block at a time, completing

two blocks/day. During filling pools were covered with tight-fitting fiberglass screen lids (1.3 x

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 11 May. Fish species were held in separate holding tanks prior to

the experiment, and we haphazardly sampled predators from these tanks (mean mass for each

species = ~3.5 g). On 11 May each patch received fish at an initial density of ~2.3 g/100 L; small

patches 2 *N. crysoleucus* + 2 *L. cyanellus*, medium received 4–5 *N. crysoleucus* + 4-5 *L.*

cyanellus, and large received 10 *N. crysoleucus* + 10 *L. cyanellus*. Because medium patches

required an uneven number of fish, medium fish patches in blocks 1, 3, and 5 received 1 extra *L.*

cyanellus, while those in blocks 2, 4, and 6 received 1 extra *N. crysoleucus*. We equalized fish

density, biomass and size structure within blocks by creating 8 matched pairs consisting of 1

"large" and 1 "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 12 May, 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 exception of *Buenoa*, *Paracymus*, and

Sigara, which were identified to genus. Identifications primarily used Testa & Lago (1994),

Larson *et al.* (2000), Epler (2006), and Epler (2010). The experiment ended on 21 July, 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.

<center>*Data analysis*</center>

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 was

rescaled to the relative size of the smallest patches (Fig. 1), and we analyzed three metrics related

to richness: species-area relationships, species density, and rarefied species richness. Abundance

is a critical measure of species preferences, and 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.

1S), both of which simplify analysis of species density (Rosenzweig et al. 2011, Gotelli and

Colwell 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/unit area varies with patch size, which here speaks

to the mechanisms of community assembly at work. Conceptually, species density should be

thought of as: $(\#species/patch\ area) = (\#species/\#individuals)x(\#individuals/$

$patch\ area)$(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 hypothetical "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/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 (v 9.1.0, Colwell 2013), generating a unique rarefaction curve for

each patch (sample). Fish patches had from 15-162 colonists, and fishless 74-708. 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 ($\sqrt{X + 0.5}$) 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), 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 v. 9.4 (SAS

Institute 2016) with Type III sums of squares and $\alpha = 0.05$.

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 PERMDISP (permutational analysis of

multivariate community dispersion) 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 non-metric 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 ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$) (Baselga 2017). $\beta_{BC.BAL}$ and

$\beta_{BC.GRA}$ are the abundance-based analogs of turnover and nestedness respectively (Baselga 2017).

PERMANOVA, PERMDISP, NMDS plots, and shade plots used PRIMER 7 with

PERMANOVA+ add-on (Anderson et al. 2015; Clarke and Gorley 2015), bubble plots were

created using SigmaPlot V13. Partitioning of β-diversity used the beta.multi and

beta.multi.abund functions in the R package beta.part v1.5.0 (Baselga 2010, 2017). Data

deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.10b64m4.

Results

Our experiment was colonized by 6875 insects: 5782 individuals of 51 species of aquatic beetles (Coleoptera, 7 families) and 1093 individuals of 7 species of aquatic true bugs (Hemiptera, 4 families) (Table S1). 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 5 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,c). Hemipterans showed significant responses to both patch size and fish, but scaled abundance was highest in large, fishless patches (Table 1, Fig. 2d). The significant size × fish interaction reflected large variation among sizes in fishless patches, but not in fish patches.

Six of the 10 most abundant beetles (*C. 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 was more abundant in fish patches (*Cymbiodyta chamberlaini*), but this was not significant (Table S1, Fig. 3a). Four of the 10 most abundant species (*C. glyphicus, Paracymus, E. ochraceus, C. chamberlaini*) significantly preferred small patches, while three preferred Large patches (*T. collaris, T. blatchleyi,* and *L. proximus*) and one had a marginally non-significant preference for large patches (*T. lateralis*)(Table S1, Fig. 3a). Significant size × fish interactions were due to preferences for size manifesting only in fishless patches, fish patches being uniformly avoided (Table S1, 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 above (Table S1, Fig. 3a).

<center>*Assemblage structure and diversity*</center>

5324 individuals of 57 (of 58 total) species colonized fishless patches (98%), vs 1551 of 40 species in 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 non-significantly different, but with significantly different intercepts (Fig. 4a).

Species density was significantly affected by abundance, size, and the size x fish interaction, with highest species density in small patches. Size explained the largest proportion of variation independent of abundance (Table 1, Fig. 4b), while fish effects on species density were driven by abundance (Table 1, Fig. 4b). Size, but not fish, had a significant effect on rarefied species richness (Table 1, Fig. 4c). Richness showed the expected increase with area, but the flatness of accumulation curves for both raw (Fig. 4a) and rarefied richness (Fig. 4c) support the idea that preferences 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 dataset (Fig. S1), which indicate 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. 3a). Fig. 3b illustrates sorting across treatments for the entire insect assemblage. Mean α-diversity was significantly affected by size alone for all insects, size, fish, and size x fish interaction for dytiscids, and size and a marginal size × fish interaction for hydrophilids and hemipterans (Table S3, 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,S4). Interactions are undefined for PERMDISP, thus each main effect was analyzed separately (mean and SE in Table S4 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 (Table 2,S4, Figs. 5b,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 S4, Figs. 5b,6). For hemipterans, location was significant for size, fish, and the interaction, and dispersion was significantly different for size only (Tables 2,S4, Figs. 5b,6), but results should be viewed with caution due 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 (Figure 7, Table S5). 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% of β-diversity (full design), 83% (fish patches), and 86% (fishless). For abundance-based measures, turnover accounted for 85%, 83%, and 78% for the full design, fish, and fishless patches respectively. The only exceptions were the less species-rich hemipterans 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 on 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 utilize it (Fretwell and Lucas 1970), and are susceptible to ecological traps (Delibes et al. 2001*b*, 2001*a*). Nonetheless, colonization decisions inform us as to 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 gradient of patch sizes. Hemipterans

strongly preferred fishless patches, and, in contrast to beetles, uniformly preferred large patches.

Thus, 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 increase in species richness with area (Fig. 4a,b).

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 >five-fold

increase in patch area, rarefied richness 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. S1). 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*b*), and strong active preferences for different patch

sizes that favors small patches overall (Fig. 2). Ryberg and Chase (2007) showed that extinction

rates/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

affected immigration rates. Here we see an increase in species richness with area, but also clear

differences in both 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 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 & Binckley 2009; Resetarits & Pintar 2016; this study), but may avoid other labile predators whose arrival is unpredictable, (e.g., *N. irrorata*: unpubl. data) as well as other large insect predators, by choosing smaller patches (Spencer et al. 1999). Even our largest mesocosms (5.73 m^2) 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 effect 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 (Table 2,S4, Fig. 6), though the effect on species density was driven by differences in abundance. Surprisingly, α-diversity differed between fish and fishless patches only for dytiscids, though there are interactions or marginal interactions with patch size for hydrophilids, dytiscids, and hemipterans (Table S3, 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 post-colonization stage, and that colonization of fish patches is more stochastic. We suggest that colonization with respect to fish for non-avoiding species is haphazard, while the colonization of fish patches by avoiding species is largely the result of recognition/reaction errors - mistakes. The differing dynamics of pre- vs post colonization sorting warrants further attention.

However, most unexpected were the significant, and counterintuitive, 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 the greater β-diversity resulted from "spillover" of species with preferences for either large or small patches. All taxa with strong preference 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,c), 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 S5). Nestedness, in the context of dispersal and colonization, implies that variation in diversity is a function of random colonization, whereas species turnover suggests non-random 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 debate over relative importance of patch quantity vs 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*b*) 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; McPeek 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 how communities are 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 (unpubl. 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 2014; Vonesh et al. 2009; Resetarits and Binckley 2009; Kraus and

Vonesh 2010; Deans and Chalcraft 2017; Pintar and Resetarits 2017*b*, 2017*a*, 2017*c*). 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 behaviourally 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 pre-empting post-colonization

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 process of community assembly, 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 as a driver of diversity.

Acknowledgments

Appendix from W. J. Resetarits, Jr. et al. "Patch size as a niche dimension: aquatic insects behaviorally partition enemy-free space across gradients of patch size"

Additional statistical tables and overall rarefaction curve.

Table A1. Species, abundance, and family for Coleoptera (51 species) and Hemiptera (7 species).

Taxa	Abundance	Taxa	Abundance
Coleoptera	5782		
Dytiscidae	2460	**Hydraenidae**	4
Acilius fraternus	5	*Hydraena marginicollis*	4
Acilius mediatus	2	**Hydrochidae**	14
Bidessonotus inconspicuus	3	*Hydrochus neosquamifer*	3
Celina angustata	15	*Hydrochus rugosus*	11
Copelatus chevrolati renovatus	2	**Hydrophilidae**	3236
Copelatus glyphicus	1932	*Berosus exiguus*	21
Coptotomus loticus	7	*Berosus infuscatus*	852
Cybister fimbriolatus	2	*Berosus pantherinus*	2
Desmopachria	10	*Berosus peregrinus*	4
Hydrocolus deflatus	1	*Berosus sayi*	17
Hydrocolus oblitus	11	*Cymbiodyta chamberlaini*	233
Hydroporus rufilabris	20	*Cymbiodyta vindicata*	5
Ilybius biguttulus	3	*Derallus altus*	42
Ilybius gagates	4	*Enochrus consors*	3
Laccophilus fasciatus rufus	227	*Enochrus fimbriatus*	21
Laccophilus proximus	82	*Enochrus ochraceus*	267
Matus bicarinatus	1	*Enochrus pygmaeus nebulosus*	10
Meridiorhantus calidus	1	*Helochares maculicollis*	41
Neoporus blanchardi	51	*Helocombus bifidus*	2
Neoporus undulatus	2	*Hydrochara soror*	15
Platambus flavovittatus	2	*Paracymus*	406
Thermonectus basillaris basillaris	41	*Tropisternus blatchleyi*	338
Uvarus granarius	19	*Tropisternus collaris*	333
Uvarus lacustris	17	*Tropisternus lateralis nimbatus*	621
Haliplidae	44	*Tropisternus natator*	3
Peltodytes dunavani	1	**Noteridae**	2
Peltodytes sexmaculatus	43	*Hydrocanthus oblongus*	2
Helophoridae	22		
Helophorus linearis	22		
Hemiptera	1093		
Corixidae	455	**Notonectidae**	595
Hesperocorixa vulgaris	366	*Buenoa*	83
Sigara	89	*Notonecta indica*	15
Gerridae	41	*Notonecta irrorata*	497
Limnoporus canaliculatus	41		
Nepidae	2		
Ranatra buenoi	2		

Table A2. Fixed effects results (Type III) from mixed model ANOVAs on responses for 14 most abundant taxa. Taxon order as in Fig. 3a. Bold indicates significance, italics indicates marginally non-significant effects. See Figure 3a for direction and magnitude of effects.

Source	df_N	df_D	F	p	Source	df_N	df_D	F	p
Coleoptera									
Copelatus glyphicus					*Tropisternus blatchleyi*				
size	2	25	36.50	**<.0001**	size	2	25	15.65	**<.0001**
fish	1	25	46.49	**<.0001**	fish	1	25	0.00	0.9447
size×fish	2	25	3.28	*0.0541*	size×fish	2	25	0.98	0.3898
Paracymus					*Laccophilus proximus*				
size	2	25	18.94	**<.0001**	size	2	25	5.72	**0.0090**
fish	1	25	51.17	**<.0001**	fish	1	25	4.03	*0.0556*
size×fish	2	25	9.83	**0.0007**	size×fish	2	25	3.57	**0.0434**
Enochrus ochraceus									
size	2	25	17.92	**<.0001**	**Hemiptera**				
fish	1	25	10.11	**0.0039**	*Notonecta irrorata*				
size×fish	2	25	3.63	**0.0413**	size	2	25	6.38	**0.0058**
Cymbiodyta chamberlaini					fish	1	25	4.15	*0.0523*
size	2	25	7.26	**0.0033**	size×fish	2	25	0.79	0.4648
fish	1	25	0.35	0.5617	**Sigara**				
size×fish	2	25	1.32	0.2863	size	2	25	26.49	**<.0001**
Berosus infuscatus					fish	1	25	33.23	**<.0001**
size	2	25	0.36	0.7041	size×fish	2	25	20.10	**<.0001**
fish	1	25	37.46	**<.0001**	*Hesperocorixa vulgaris*				
size×fish	2	25	0.19	0.8302	size	2	25	23.69	**<.0001**
Laccophilus fasciatus					fish	1	25	20.50	**0.0001**
size	2	25	0.99	0.3863	size×fish	2	25	15.17	**<.0001**
fish	1	25	12.13	**0.0018**	*Buenoa*				
size×fish	2	25	10.21	**0.0006**	size	2	25	10.62	**0.0005**
Tropisternus lateralis					fish	1	25	9.71	**0.0046**
size	2	25	2.86	*0.0760*	size×fish	2	25	9.71	**0.0008**
fish	1	25	18.58	**0.0002**					
size×fish	2	25	1.00	0.3838					
Tropisternus collaris									
size	2	25	11.67	**0.0003**					
fish	1	25	2.87	0.1024					
size×fish	2	25	0.57	0.5750					

Table A3. Fixed effects results (Type III) from mixed model ANOVAs on patch level α-diversity (effective numbers) for all insects and component taxonomic groups. Bold indicates significance, italics indicate marginally non-significant effects. Different df for hemipterans inclusion of non-zero estimated block effect in the model.

Source	df_N	df_D	F	p
All insects				
size	2	30	27.47	**<.0001**
fish	1	30	2.66	0.1131
size×fish	2	30	0.62	0.5442
Hydrophilids				
size	2	30	3.66	**0.0379**
fish	1	30	1.04	0.3167
size×fish	2	30	3.01	*0.0642*
Dytiscids				
size	2	30	12.26	**0.0001**
fish	1	30	18.66	**0.0002**
size×fish	2	30	9.40	**0.0007**
Hemipterans				
size	2	25	39.83	**<.0001**
fish	1	25	3.16	*0.0875*
size×fish	2	25	0.49	0.6181

Table A4. - PERMANOVA results for average similarity between treatments, and PERMDISP results for mean multivariate dispersion. Bold indicates significant effects or significantly different treatments. Italics indicate within treatment similarities for PERMANOVA. [§]PERMDISP results for Hemiptera should be viewed cautiously because of empty cells.

a) All insects (S = 58, N = 6875)
PERMANOVA
Average Similarity between/within groups

	LNF	LF	MNF	MF	SNF	SF
Large, no fish	*67.57*					
Large, fish	**51.34**	*64.31*				
Medium, no fish	**50.58**	**46.77**	*52.59*			
Medium, fish	**38.89**	**55.85**	**40.54**	*58.91*		
Small, no fish	**42.28**	**36.77**	**53.98**	**33.48**	*66.14*	
Small, fish	**38.59**	**43.08**	**48.48**	**38.85**	**48.74**	*57.05*

PERMDISP *Mean dispersion*

Group	Size	Average	SE
Large, no fish	6	21.168	1.4286
Large, fish	6	23.043	2.4998
Medium, no fish	6	30.457	3.5348
Medium, fish	6	26.452	3.0729
Small, no fish	6	21.88	1.2064
Small, fish	6	28.191	1.5662

b) Hydrophilids (S = 20, N = 3236)
PERMANOVA
Average Similarity between/within groups

	LNF	LF	MNF	MF	SNF	SF
Large, no fish	*67.51*					
Large, fish	**62.26**	*69.58*				
Medium, no fish	**55.55**	**49.59**	*56.15*			
Medium, fish	**58.03**	66.21	**47.99**	*63.36*		
Small, no fish	**48.61**	**40.87**	58.67	**40.41**	*68.27*	
Small, fish	**35.89**	**42.22**	**45.33**	**41.69**	**45.00**	*47.36*

PERMDISP *Mean dispersion*

Group	Size	Average	SE
Large, no fish	6	21.386	2.3125
Large, fish	6	19.386	3.2939
Medium, no fish	6	27.582	4.6234
Medium, fish	6	23.756	3.2533
Small, no fish	6	20.552	1.6014
Small, fish	6	34.524	3.3401

c) Dytiscids (S = 24, N = 2460)
PERMANOVA
Average Similarity between/within groups

	LNF	LF	MNF	MF	SNF	SF
Large, no fish	*69.14*					
Large, fish	**47.77**	*67.07*				
Medium, no fish	**54.92**	**44.56**	*52.19*			
Medium, fish	**31.24**	**52.59**	**33.36**	*60.38*		
Small, no fish	**45.63**	**33.9**	**51.93**	**23.89**	*67.28*	
Small, fish	**60.05**	**51.89**	60.5	**38.73**	**56.59**	*75.41*

PERMDISP *Mean dispersion*

Group	Size	Average	SE
Large, no fish	6	20.147	1.5141
Large, fish	6	21.384	1.5861
Medium, no fish	6	31.129	3.601
Medium, fish	6	25.286	4.7529
Small, no fish	6	21.249	1.1193
Small, fish	6	16.22	1.8514

d) Hemipterans (S = 7, N = 1093)
PERMANOVA
Average Similarity between/within groups

	LNF	LF	MNF	MF	SNF	SF
Large, no fish	*67.3*					
Large, fish	**38.79**	*46.06*				
Medium, no fish	**39.15**	51.27	*45.03*			
Medium, fish	**20.27**	**35.76**	**27.73**	*53.37*		
Small, no fish	**26.56**	**39.42**	**35.89**	**26.53**	*64.04*	
Small, fish	**24.23**	40.58	**35.95**	**25.6**	74.7	*77.56*

[§]**PERMDISP** *Mean dispersion*

Group	Size	Average	SE
Large, no fish	6	21.562	1.9663
Large, fish	6	34.704	6.0571
Medium, no fish	4	33.638	5.6345
Medium, fish	4	29.348	3.8654
Small, no fish	4	21.802	4.6328
Small, fish	3	13.426	3.7884

Table A5. Total multisite β – diversity based on presence/absence data (Sorenson - β_{SOR}) partitioned between additive components attributable to species turnover (β_{SIM}) and nestedness (β_{NES}) , and total β – diversity based on abundance data (Bray-Curtis - β_{BC}) partitioned between additive components attributable to balanced variation ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$).

All insects

	Presence/absence	**Abundance**
Full design	$\beta_{SOR} = 0.897$	$\beta_{BC} = 0.932$
	$\beta_{SIM} = 0.794$	$\beta_{BC.BAL} = 0.790$
	$\beta_{NES} = 0.104$	$\beta_{BC.GRA} = 0.142$
Fish	$\beta_{SOR} = 0.813$	$\beta_{BC} = 0.870$
	$\beta_{SIM} = 0.677$	$\beta_{BC.BAL} = 0.724$
	$\beta_{NES} = 0.137$	$\beta_{BC.GRA} = 0.146$
Fishless	$\beta_{SOR} = 0.807$	$\beta_{BC} = 0.858$
	$\beta_{SIM} = 0.691$	$\beta_{BC.BAL} = 0.672$
	$\beta_{NES} = 0.116$	$\beta_{BC.GRA} = 0.186$

Hydrophilidae

	Presence/absence	**Abundance**
Full design	$\beta_{SOR} = 0.876$	$\beta_{BC} = 0.935$
	$\beta_{SIM} = 0.759$	$\beta_{BC.BAL} = 0.808$
	$\beta_{NES} = 0.116$	$\beta_{BC.GRA} = 0.128$
Fish	$\beta_{SOR} = 0.777$	$\beta_{BC} = 0.867$
	$\beta_{SIM} = 0.563$	$\beta_{BC.BAL} = 0.655$
	$\beta_{NES} = 0.214$	$\beta_{BC.GRA} = 0.212$
Fishless	$\beta_{SOR} = 0.770$	$\beta_{BC} = 0.882$
	$\beta_{SIM} = 0.671$	$\beta_{BC.BAL} = 0.752$
	$\beta_{NES} = 0.099$	$\beta_{BC.GRA} = 0.131$

Dytiscidae

	Presence/absence	**Abundance**
Full design	$\beta_{SOR} = 0.917$	$\beta_{BC} = 0.908$
	$\beta_{SIM} = 0.812$	$\beta_{BC.BAL} = 0.560$
	$\beta_{NES} = 0.105$	$\beta_{BC.GRA} = 0.349$
Fish	$\beta_{SOR} = 0.838$	$\beta_{BC} = 0.781$
	$\beta_{SIM} = 0.719$	$\beta_{BC.BAL} = 0.508$
	$\beta_{NES} = 0.119$	$\beta_{BC.GRA} = 0.273$
Fishless	$\beta_{SOR} = 0.842$	$\beta_{BC} = 0.804$
	$\beta_{SIM} = 0.720$	$\beta_{BC.BAL} = 0.368$
	$\beta_{NES} = 0.122$	$\beta_{BC.GRA} = 0.436$

Hemiptera

	Presence/absence	**Abundance**
Full design	$\beta_{SOR} = 0.918$	$\beta_{BC} = 0.958$
	$\beta_{SIM} = 0.564$	$\beta_{BC.BAL} = 0.636$
	$\beta_{NES} = 0.354$	$\beta_{BC.GRA} = 0.321$
Fish	$\beta_{SOR} = 0.878$	$\beta_{BC} = 0.921$
	$\beta_{SIM} = 0.549$	$\beta_{BC.BAL} = 0.544$
	$\beta_{NES} = 0.329$	$\beta_{BC.GRA} = 0.377$
Fishless	$\beta_{SOR} = 0.833$	$\beta_{BC} = 0.937$

$\beta_{SIM} = 0.262$ $\beta_{BC.BAL} = 0.593$

$\beta_{NES} = 0.570$ $\beta_{BC.GRA} = 0.34$

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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-d). Bold indicates significance. Different df for species density reflect removal of zero estimated block effect from the model. See Table 1S and Fig. 3a for individual species results.

Species density

Source	df_N	df_D	F	p
abundance	1	29	14.81	**0.0006**
size	2	29	74.53	**<.0001**
fish	1	29	1.55	0.2235
size*fish	2	29	6.56	**0.0045**

Rarefied species richness

size	2	25	13.96	**<.0001**
fish	1	25	0.26	0.6122
size*fish	2	25	1.45	0.2546

Abundance

All insects

size	2	25	15.01	**<.0001**
fish	1	25	69.49	**<.0001**
size*fish	2	25	0.1	0.9027

Hydrophilids

size	2	25	4.58	**0.0202**
fish	1	25	26.41	**<.0001**
size*fish	2	25	0.37	0.692

Dytiscids

size	2	25	34.8	**<.0001**
fish	1	25	66.67	**<.0001**
size*fish	2	25	1.55	0.2326

Hemipterans

size	2	25	45.4	**<.0001**
fish	1	25	30.74	**<.0001**
size*fish	2	25	13.79	**<.0001**

Table 2. - PERMANOVA results for multivariate location (average community composition) and PERMDISP results for multivariate dispersion (broad sense β-diversity) for size and fish treatments analyzed separately (Figs. 5b,6). All p values based on data permutations. Bold indicates significant effects. §PERMDISP results for Hemiptera should be viewed cautiously because of missing values (due to patches with no Hemiptera) creating an unbalanced design.

a) All insects (S = 58, N = 6875)
PERMANOVA

Source	df	SS	MS	Pseudo-F	P
Size	2	13850	6924.9	8.55	**0.001**
Fish	1	8997.1	8997.1	11.11	**0.001**
SizexFish	2	5035.8	2517.9	3.11	**0.001**
Res	30	24304	810.12		
Total	35	52186			

PERMDISP
Size $F_{1,33} = 4.836, P = \textbf{0.018}$
Fish $F_{1,34} = 0.349, P = 0.602$

b) Hydrophilids (S = 20, N = 3236)

PERMANOVA

Source	df	SS	MS	Pseudo-F	P
Size	2	11685	5842.5	7.16	**0.001**
Fish	1	7505.3	7505.3	9.19	**0.001**
SizexFish	2	2806.1	1403.1	1.72	0.074
Res	30	24492	816.39		
Total	35	46488			

PERMDISP
Size $F_{2,33} = 4.814, P = \textbf{0.027}$
Fish $F_{1,34} = 0.678, P = 0.475$

c) Dytiscids (S = 24, N = 2460)
PERMANOVA

Source	df	SS	MS	Pseudo-F	P
Size	2	12787	6393.3	9.37	**0.001**
Fish	1	11307	11307	16.57	**0.001**
SizexFish	2	6717.2	3358.6	4.92	**0.001**
Res	30	20468	682.28		
Total	35	51279			

PERMDISP
Size $F_{2,33} = 15.156, P = \textbf{0.001}$
Fish $F_{1,34} = 0.1037, P = 0.774$

d) Hemipterans (S = 7, N = 1093)
PERMANOVA

Source	df	SS	MS	Pseudo-F	P
Size	2	19193	9596.6	8.94	**0.001**
Fish	1	4904.5	4904.5	4.57	**0.003**
SizexFish	2	7650.3	3825.2	3.56	**0.003**
Res	21	22550	1073.8		
Total	26	55396			

§PERMDISP
Size $F_{2,24} = 7.201, P = \textbf{0.013}$
Fish $F_{1,25} = 0.004, P = 0.942$

Figure 1. Schematic of experimental layout. Patch size approximately to scale. Blue = fishless, Red = fish. Enclosing line indicates edge of an oldfield surrounded by mixed forest.

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

Figure 3. a) Bubble plot of proportion of each species in fish vs fishless patches (left) and patches of different size (right), for the 14 most abundant species (≥ 72 individuals total). Data from ANOVA on transformed ($\sqrt{X + 0.5}$) abundances using Fisher's Protected LSD. Left panel shows main effect of fish, right panel main effect of size. ** = p < 0.01, MS = 0.05 < p < 0.1, NS = p > 0.1 (ANOVA details in Table S2). Solid arrows indicate significant fish x size interaction (p < 0.05), open arrows marginal interaction (0.05 < p < 0.1). Top 10 species are Coleoptera, **§** = Dytiscidae, others = Hydrophilidae, bottom 4 are Hemiptera. b) Shade plot (heat map) showing squareroot transformed abundances for the entire insect assemblage. Warmer colors indicate greater abundance. Treatment symbols: red = fish, blue = fishless, size of circle indicates patch size. Treatments ordered by similarity, and species order is based on similarity of distribution (See Table 2, Fig. 6).

Figure 4. Fish patches = red, fishless patches = blue. a) Insect species/area relationships and best fit regression lines plotting raw species richness vs patch size for fish and fishless patches. b) uncorrected insect species density (mean ± 1SE) (species per unit area - see Methods) showing results of ANCOVA with abundance as 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 ± 1SE) (see Methods). Note relative flatness of species-area relationships in a and c (see Discussion).

Figure 5. a) α-diversity (effective numbers based on Shannon index)(mean ± 1SE) and b) β - diversity (multivariate community dispersion based on Bray-Curtis) (mean ± 1 SE) (see Fig. 6 for NMDS plots), by treatment for the 4 taxonomic groups. S,M,L = small, medium and large; F,NF = fish, no fish. Numbers in parentheses indicate number of species. Factors above bars are statistically significant, those in italics marginally non-significant. See Tables 2,S3,S4) for detailed statistics.

Figure 6. NMDS plots visualizing assemblages by size/fish treatment combinations: a) All insects, b) hydrophilids, c) dytiscids, d) hemipterans. 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 PERMANOVA and PERMDISP statistics see Tables 2 (main effects),S4 (pairwise comparisons and treatment dispersion means).

Figure 7. Left: total multisite β – diversity based on presence/absence data (Sorenson - β_{SOR}) partitioned between additive components attributable to species turnover (β_{SIM} = hatched) and nestedness (β_{NES} = solid) , and **Right**: total β – diversity based on abundance data (Bray-Curtis - β_{BC}) partitioned between additive components attributable to balanced variation ($\beta_{BC.BAL}$ = hatched) and abundance gradients ($\beta_{BC.GRA}$ = solid). $\beta_{BC.BAL}$ and $\beta_{BC.GRA}$ 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 fish (red) and fishless (blue) 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 S5 for detailed statistics.

Figure S1. Rarefaction curve for all insects, with 95% confidence limits. The largest patch value from the experiment (large, fishless patch) is shown. Patches were individually rarefied for analysis: this figure simply illustrates where our samples fell on the overall rarefaction curve, indicating that for the range of abundances in our experiment the species abundance curve was roughly linear, and richness in the largest samples was not greatly constrained by the total species pool.
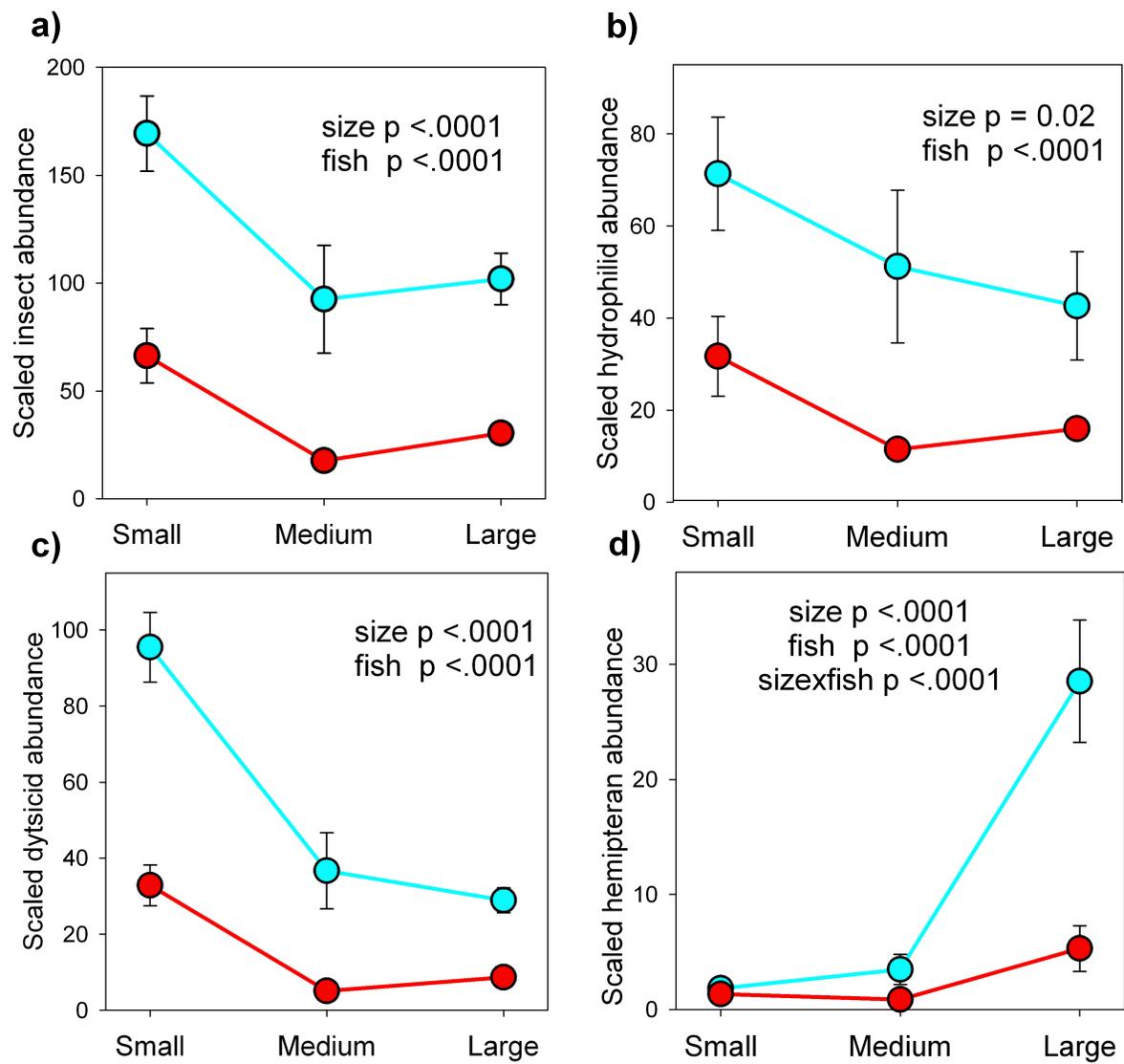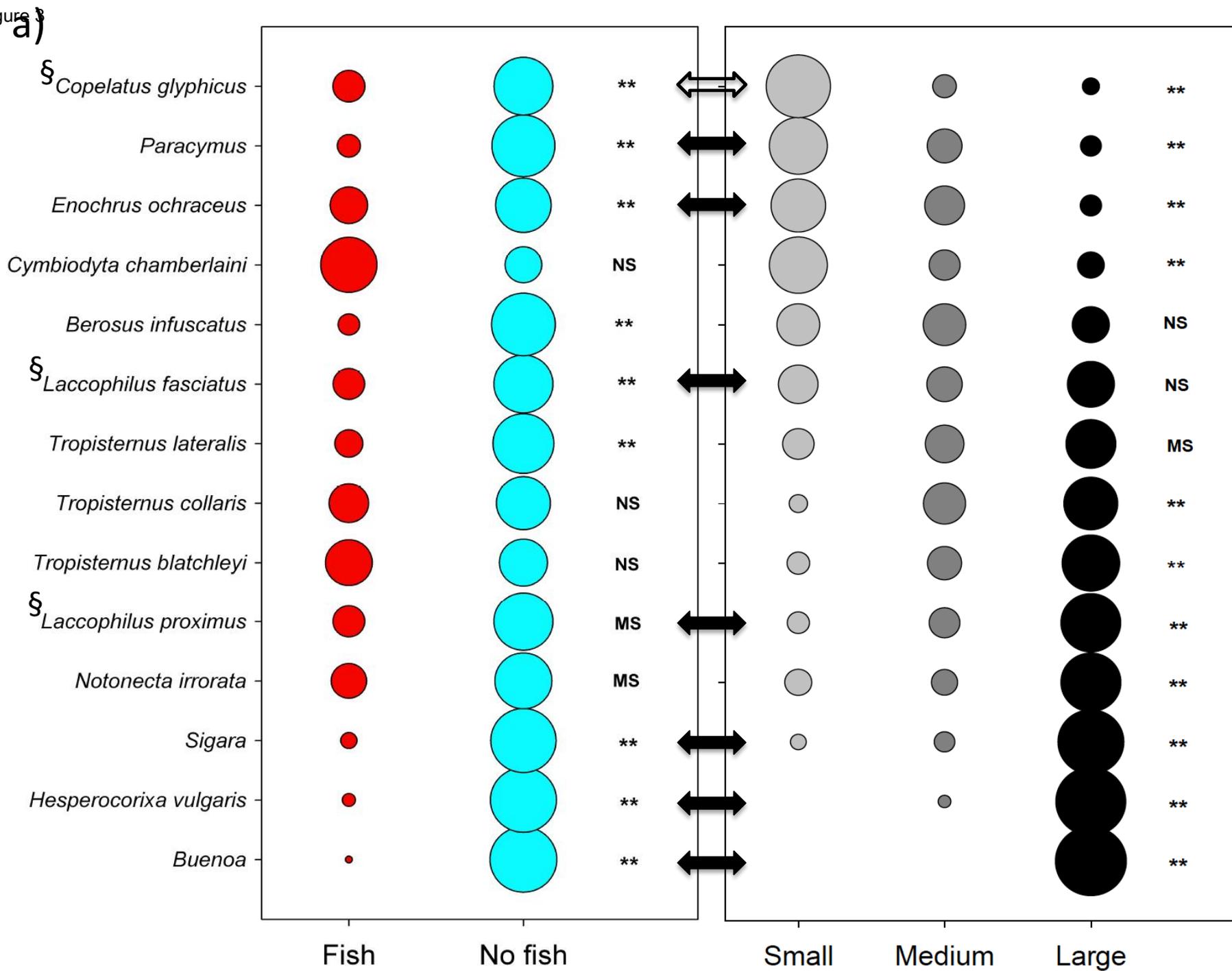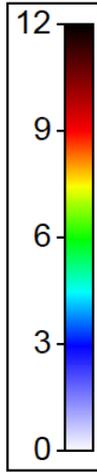
Figure 1

TRT	Area	Litter	#Fish
○	1.13 m²	0.9kg	
○	2.54 m²	2.0kg	
③	5.73 m²	4.4kg	
●	1.13 m²	0.9kg	4
●	2.54 m²	2.0kg	9
③	5.73 m²	4.4kg	20

N

> 10 m

5 m

5 m

Figure 2

Figure 3

a)

	Fish	No fish			Small	Medium	Large	
§ *Copelatus glyphicus*			**	⇔				**
Paracymus			**	⬌				**
Enochrus ochraceus			**	⬌				**
Cymbiodyta chamberlaini			NS					**
Berosus infuscatus			**					NS
§ *Laccophilus fasciatus*			**	⬌				NS
Tropisternus lateralis			**					MS
Tropisternus collaris			NS					**
Tropisternus blatchleyi			NS					**
§ *Laccophilus proximus*			MS	⬌				**
Notonecta irrorata			MS					**
Sigara			**	⬌				**
Hesperocorixa vulgaris			**	⬌				**
Buenoa			**	⬌				**

b)

Species (heatmap, vertical axis, top to bottom):

Hydrocolus deflatus
Copelatus chevrolati
Enochrus perplexus
ssonotus inconspicuus
Desmopachria leechi
Cymbiodyta vindicata
Acilius mediatus
Agabus gagates
Helocombus bifidus
Berosus exiguus
Hydroporus niger
Hydrocolus oblitus
Enochrus pygmaeus
Neoporus blanchardi
Laccophilus fasciatus
Uvarus granarius
Paracymus
Enochrus ochraceus
Copelatus glyphicus
mbiodyta chamberlaini
Hydrochus rugosus
Derallus altus
Helopohorus linearis
Berosus striatus
Helochares maculicollis
Hydrochara soror
Berosus infuscatus
Tropisternus lateralis
Laccophilus proximus
Tropisternus blatchleyi
Tropisternus collaris
Limnoporus canaliculatus
Hesperocorixa vulgaris
Sigara
Thermonectus basillaris
Peltodytes sexmaculatus
Buenoa
Notonecta indica
Platambus astrictovittatus
Notonecta irrorata
Celina angustata
Cybister fimbriolatus
Acilius fraternus
Rhantus calidus
Ilybius biguttulus
Hydraena marginicollis
Hydrocanthus oblongus
Enochrus consors
Coptotomus loticus
Neoporus undulatus
Matus bicarinatus
Ranatra buenoi
Uvarus lacustris
Hydrochus neosquamifer
Berosus peregrinus
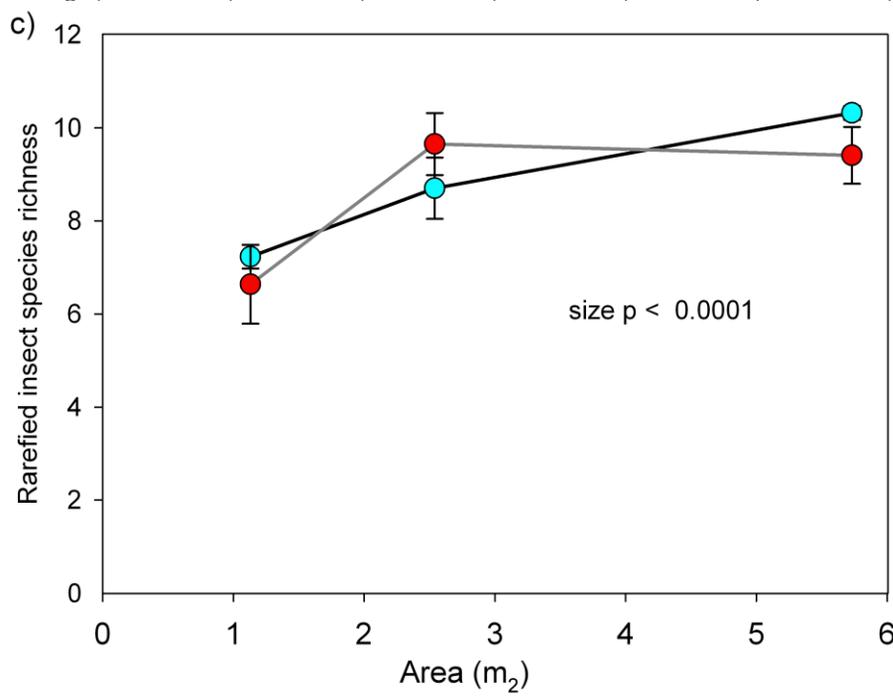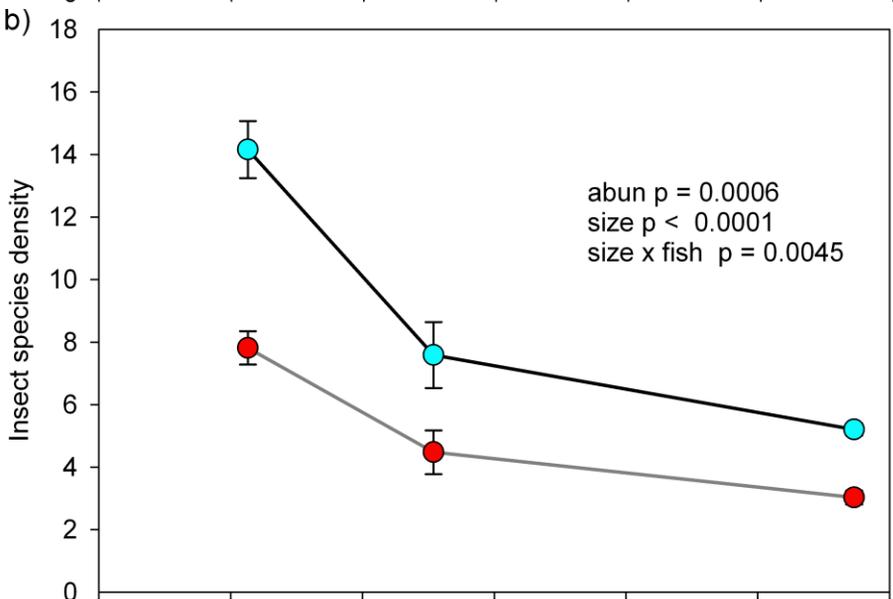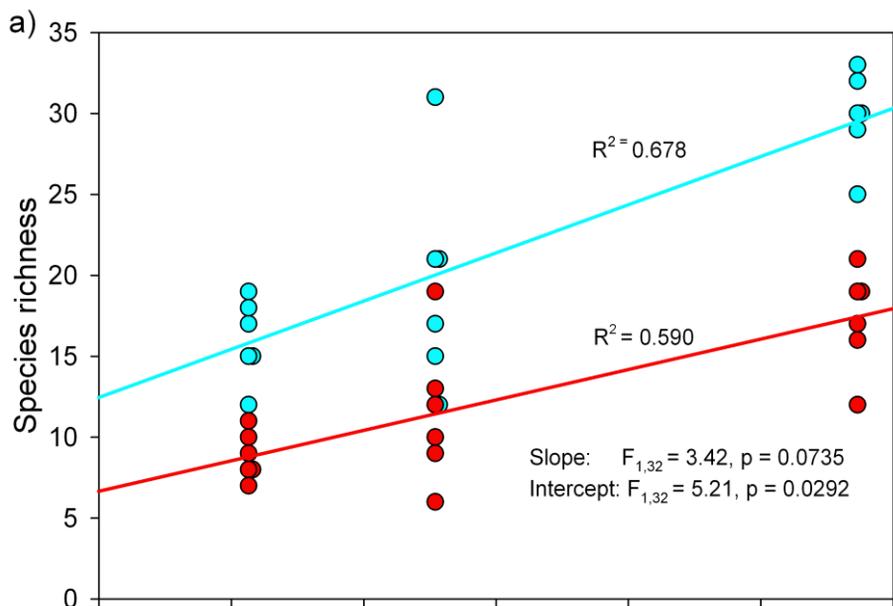*Berosus pantherinus*
Tropisternus natator
Peltodytes dunavani

Color scale legend: 0, 3, 6, 9, 12

Figure 4

a)

R^2 = 0.678

R^2 = 0.590

Slope: F$_{1,32}$ = 3.42, p = 0.0735
Intercept: F$_{1,32}$ = 5.21, p = 0.0292

Species richness

b)

abun p = 0.0006
size p < 0.0001
size x fish p = 0.0045

Insect species density

c)

size p < 0.0001

Rarefied insect species richness

Area (m$_2$)

Figure 5

Figure 6

Figure 7