



# Temperature but not nutrient addition affects abundance and assemblage structure of colonizing aquatic insects

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**Abstract.** Abiotic conditions are important considerations in the species sorting process, which ultimately determines the distribution and abundance of species. Freshwater ecosystems will be impacted by ongoing temperature rise and other anthropogenically induced changes, such as nutrient enrichment and eutrophication. Changing characteristics of freshwater habitats will likely impact organisms in numerous ways, including through effects on colonization dynamics. Species are expected to colonize habitat patches where fitness will be the highest for themselves and their offspring, and how habitat selection interacts with changing environments remains an important question. We conducted a warming experiment to test the habitat selection preferences of aquatic beetles and hemipterans between habitat patches (mesocosms) of varying temperatures (via heaters), nutrient addition, and their interaction. Overall, insect abundance and richness were higher in unheated patches, with taxon-specific variation in response to heating. Although nutrients had limited effects on environmental conditions in mesocosms, their addition had no significant effects on insects. Insect assemblages had unique structures across heating treatments, with lower beta diversity and higher effective numbers of species in the warmest mesocosms. Our data support the importance of spatial variation in abiotic factors during the habitat selection process, and in determining species distributions and abundances as shallow lentic ecosystems are impacted by rising global temperatures.

**Key words:** aquatic insects; aquatic Heteroptera; climate change; colonization; community assembly; Dytiscidae; eutrophication; habitat selection; Hydrophilidae; patch quality; thermoregulation; water beetles.

## INTRODUCTION

The processes that determine the distribution and abundance of species are of fundamental interest in ecology (Andrewartha and Birch 1954). Biotic factors such as predation (Paine 1966, Wellborn et al. 1996) and competition (Shurin and Allen 2001) can play critical roles in generating patterns of biodiversity, but abiotic conditions such as temperature and nutrient availability may initially be more important in the sorting process, especially in freshwater habitats (Diamond and Reice 1985, Laprise and Dodson 1994, McCreddie and Adler 2012). Temperature plays a vital role in processes that occur at all biological levels (Brown et al. 2004, Angilletta 2009), and thermosensation is among the most essential sensory functions in animals (Mizunami et al. 2016).

Mechanisms of thermosensation and many thermoregulatory behaviors have been extensively studied in insects and other ectotherms (Lee and Denlinger 1991, Gilbert and Raworth 1996). Abram et al. (2017) placed thermoregulatory behaviors in four broad categories: microhabitat selection, basking, modification of temporal activity cycles, and transient endothermy. Insects can use any one or combination of these strategies to achieve their desired temperature, but larger-scale, demographic habitat selection (among discrete habitat patches) has rarely been considered (Huey 1991).

Temperature within a lentic freshwater habitat patch can vary tremendously, both spatially among microhabitats and temporally throughout the day (Ward and Stanford 1982), however, the complex life cycles of many ectotherms that use these habitats necessitate that at some time adults will cross the terrestrial matrix and choose among aquatic habitat patches that vary in numerous characteristics, including patch temperature regime. Selection of a habitat patch precedes, and supersedes, many of the other thermoregulatory behaviors, given the limited ability (or inability) of offspring, or even some adults, to move among habitats after initial colonization. Even for species capable of leaving unfavorable habitats, dispersal is energetically

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expensive and risky (Zera and Denno 1997), placing increased emphasis on initial colonization and oviposition decisions.

With rising global temperatures, there is added interest and need to understand thermal responses within species and across communities. Aquatic insects, and beetles in particular, form diverse assemblages that can account for a large portion of the biomass and species richness in aquatic habitats, and they can be ecologically important as indicators of habitat quality (Fairchild et al. 2003). These species have a wide range of physiological, morphological, and behavioral characteristics that cause differences in their tolerance of environmental variation, dispersal abilities, and habitat preferences (Chown and Terblanche 2006). Air-breathing adult beetles and hemipterans may be able to avoid some of the negative aspects of nutrient enrichment, such as lower dissolved oxygen levels, and take advantage of higher resource availability in these habitats. Indeed, many colonizing beetles respond positively to nutrients (Pintar and Resetarits 2017c), while water temperature can be an important determinant of geographic ranges of some species (Calosi et al. 2010). However, studies of interactions among environmental variables on habitat selection are lacking in many systems (Rieger et al. 2004, Pintar et al. 2018).

Colonization is an especially critical process in freshwater habitats, as a large proportion of the aquatic fauna have complex life cycles that require annual, or more frequent, recolonization. Ideally, species should colonize not only habitats within their physiological tolerances, but also where they have the highest fitness within that range of tolerable environmental conditions (Pellerin et al. 2018). Habitat selection at the colonization stage can be a direct response to unfavorable conditions where low-quality patches are avoided (Fretwell and Lucas 1969, Pulliam and Danielson 1991). In most systems, temperature and resource availability are two of the most important abiotic factors that determine habitat quality and the distribution of organisms (Magnuson et al. 1979, John et al. 2007).

Rising temperatures of shallow lentic systems (Butcher et al. 2017) can have direct impacts on species if temperatures are already near critical thermal maxima, as well as indirect effects resulting from shifts in water quality and resources (Komatsu et al. 2007, Dallas and Rivers-Moore 2012). Oxygen is less soluble in warmer waters, which can change species interactions and the resulting food web, as many gilled organisms are unable to persist (Verberk and Bilton 2013), creating additional habitat space for species that typically avoid habitats with gilled predators such as fish and amphibian larvae. Hydroperiod of freshwater habitats might decrease as temperatures increase due to increased evaporation, although hydroperiod is more strongly influenced by precipitation, changes that can be more difficult to predict (Stocker et al. 2013). Warmer water can also increase primary production and internal

nutrient loading through increased decomposition and mineralization rates, which amplifies the negative effects of external nutrient input from runoff and can cause aquatic systems to flip to a eutrophic state, causing shifts in the water chemistry, resources, and species composition (Jensen and Anderson 1992, Liikanen et al. 2002).

Eutrophic lakes have high levels of nitrogen and phosphorus, favoring floating plants and phytoplankton, and low periphyton abundances and dissolved oxygen levels. These conditions allow dominance by a few tolerant species, often resulting in lower biodiversity (Feuchtmayr et al. 2009). This could impact many species with complex life cycles, such as insects and amphibians, that rely on aquatic habitats for their larval stages. For many of these taxa, gilled, fully aquatic larval stages have limited, if any, dispersal capabilities and are more susceptible to conditions in aquatic habitats than adults (Hoback and Stanley 2001). These evolutionary life history constraints limit dispersal to particular life history stages (adults, and often immediately after eclosion), making habitat selection and oviposition choices of adults important for adult and offspring survival (Resetarits 1996, Morris 2003).

We conducted a warming experiment in naturally colonized experimental landscapes to determine the effects of water temperature (via heaters) and nutrient addition on colonization by adult beetles and hemipterans, and assess the resulting species composition of insect colonists. We hypothesized that under an adaptive decision-making framework, colonizing insects would select patches based on both nutrient availability and water temperature, resulting in different species composition among treatments. We predicted preference for habitats with added nutrients, based on prior studies. However, given the lack of work on the effect of temperature on aquatic beetles, we were unsure how temperature would affect habitat preferences, although predictions could be made for either higher or lower temperature preferences based on shortened developmental times or thermal tolerances, respectively.

## MATERIALS AND METHODS

Our experiment was conducted at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi, USA during the summer of 2018. There is a diverse assemblage of aquatic insects at UMFS, including 132 species of aquatic beetles and over 40 species of aquatic/semiaquatic hemipterans (Pintar and Resetarits 2020a, b). We established 1,300-L mesocosms (plastic cattle tanks are patches; 1.83 m diameter; 36 total mesocosms) in a naturally colonized experimental landscape, allowing dispersing insects to select among and colonize individual habitat patches. The experiment was a fully factorial complete block design crossing three levels of heating (control, 0 heaters; low heat, 1 heater; high heat, 2 heaters; Eheim Jager Aquarium Thermostat Heater 300W: Eheim, Deizisau, Germany) with two

initial levels of nutrient addition (control and added N/P reagent), resulting in six total treatments, each replicated six times. Each heater was placed near the bottom center of the mesocosms and set to maximum output. Blocks 1–2 were filled on 10 May, blocks 3–4 on 12 May, and blocks 5–6 on 15 May. To establish a nutrient base representative of smaller ponds at UMFS, all mesocosms received 1 kg of well-mixed leaf litter from the surrounding area on the day they were filled. Treatments were randomly assigned within each block, and nutrient treatments were established at the beginning of the experiment on 16 May by adding 100 mL of a nitrogen/phosphorus reagent (80  $\mu\text{g/L}$  P, 8  $\mu\text{g}$  total P per mesocosm; 1,500  $\mu\text{g/L}$  N, 150  $\mu\text{g}$  total N per mesocosm) to initially mimic high nutrient input sites in the nearby area (U.S. Environmental Protection Agency 2000). Mesocosms were 1.5 m apart, fit with standpipes to maintain water levels, and tightly fit with fiberglass screen lids ( $1.3 \times 1.13 \text{ mm}^2$  openings) that were pushed below the water surface to allow for insect colonization and efficient collection, while preventing insects from going underneath the screens.

All blocks were opened to colonization on 18 May, but due to electrical issues blocks 5 and 6 did not have working heaters until 20 May. We removed all insects that had colonized the experiment during the first two days on 20 May and excluded them from our analyses. Starting 27 May, colonizing adult insects were exhaustively collected once weekly during the morning, preserved, and identified to the lowest feasible taxonomic level (species for most, genera for a few) following Pintar and Resetarits (2020a, b). Samples were collected from all 36 mesocosms for 14 weeks. After the collections on 17 June, we stopped sorting and counting one genus, *Microvelia*, due to their increasing abundance and the difficulty in separating colonists from individuals that had not colonized mesocosms but were the offspring of colonists. The experiment was terminated on 26 August.

Once weekly, typically two days prior to insect collection, we recorded temperature, pH, and nitrate levels using a YSI Pro Plus Multiparameter Instrument (YSI, Yellow Springs, Ohio, USA). Measurements were taken 10 cm below the water surface near the center of each mesocosm, in the area above the screens where insects colonized. The pH data from the last two weeks were excluded due to miscalibration. We collected water samples to test chlorophyll *a* levels in vivo using a TD-700 Laboratory Fluorometer (Turner Designs, San Jose, California, USA) during weeks 4–15. Phosphate levels were also tested during weeks 6, 8, 10, 12, 14, and 15 using a HANNA Low Range HI-96713 Phosphate Portable Photometer (Hanna Instruments, Smithfield, Rhode Island, USA).

#### *Data analysis*

We designed the experiment with three categorical levels of heating (0, 1, or 2 heaters) that manifested itself

as variation in temperature across the experiment. We used this categorical number of heaters as an ordered ( $0 < 1 < 2$ ) predictor variable, but weekly temperature readings varied based on temporal and spatial variation in ambient temperatures and heater effectiveness. Our weekly temperature readings served to document that heaters were effective at creating variation in water temperature. Both nutrient addition (two levels) and block (six levels) were also treated as categorical variables. Additionally, for repeated-measures analyses, we treated week as a categorical variable (15 measurement dates) because we expected temporal variation across the experiment to vary from week-to-week, but not necessarily a directional change over time.

We used fully factorial repeated-measures analyses to quantify environmental variables over time; as these analyses are descriptive in nature, we did not correct *P* values for multiple tests. For these, we assessed the fixed effects of number of heaters, nutrient addition, week, and their interactions, with block and mesocosm as random effects, using repeated-measures linear mixed-effects models fit by maximum likelihood (using the Satterthwaite method) with type III sums of squares on log-transformed (except pH) environmental variables.

For insects, our primary response variables are five community (assemblage) metrics: abundance of all insects, taxonomic richness (species/genera), alpha diversity (Jost's effective number of species [inverse Simpson]; Jost 2006), assemblage structure (PERMANOVA), and beta diversity (distance to median). *Microvelia* were excluded from all community analyses due to issues mentioned previously. Because we did not necessarily expect equivalent responses among all colonizing species/genera, we separately analyzed abundances of individual species/genera with abundances > 125. Abundances of all taxa were summed across the duration of the experiment and square-root transformed ( $\sqrt{X+0.5}$ ).

To assess assemblage structure (PERMANOVA), we assessed the number of heaters, nutrient addition, and their interactions using the adonis function (vegan package v. 2.5-6; Oksanen et al. 2020) with the Bray-Curtis index, block as strata, and 9,999 permutations. We used the betadisper function to test for homogeneity of multivariate dispersions (beta diversity; distance to median), with separate analyses for the effects of number of heaters and nutrient addition. Richness, alpha diversity, and all abundance analyses included the number of heaters, nutrient addition, and their interaction as fixed effects, with block as a random effect, and were analyzed with linear mixed-effects models fit by maximum likelihood (using the Satterthwaite method) with type III sums of squares. The analysis of taxonomic richness included insect abundance as a covariate because the two are expected to positively covary. In our results, we also include *P* values for abundance analyses corrected for family-wise error rates (Benjamini-Hochberg; Benjamini and Hochberg 1995), along with estimated effect sizes

( $\eta_p^2$ ) for all analyses. However, both should be interpreted with caution as colonizing insect species are largely expected to be independent and rarely respond to each other (Pintar and Resetarits 2020c), and there are no widely accepted methods for generating effect sizes with mixed-effects models, respectively. All univariate analyses were conducted using the lme4 v 1.1-23 and lmerTest v 3.1-2 packages in R v 4.0.2 (Bates et al. 2015, Kuznetsova et al. 2017, R Core Team 2020). For visualization of community responses, NMDS was produced with metaMDS in vegan and a shadeplot was produced using PRIMER 7 (Clarke and Gorley 2015). Data are available on figshare (McNamara et al. 2020).

## RESULTS

### Environmental variables

Heaters had the desired effect of increasing temperature above background (Table 1; Appendix S1: Table S2; Fig. 1a): on average, mesocosms with one heater were  $1.11^\circ \pm 0.04^\circ\text{C}$  (mean  $\pm$  SE), and with two heaters  $4.49^\circ \pm 0.11^\circ\text{C}$ , above the average temperature of the two mesocosms without heaters within the same block. There was strong temporal variation (week) in all environmental analyses independent of treatments (Table 1). Conductivity was higher in mesocosms with more heaters, and differences between treatments increased over time (Fig. 2b). Heaters and nutrients affected pH, but with considerable variation over time and no clear patterns (Fig. 1c). Nitrate was high during the first measurement and greater in mesocosms where we added both nutrients and heaters, but it quickly declined in all mesocosms for the remainder of the experiment (Fig. 1d). We lacked chlorophyll and phosphate measurements during several weeks of the experiment, and these did not exhibit any clear pattern with nutrient addition or heaters.

### Insect responses

A total of 2,944 beetles representing 36 species/genera in five families and 1,226 hemipterans of 7 species/genera in five families colonized our experiment (Appendix

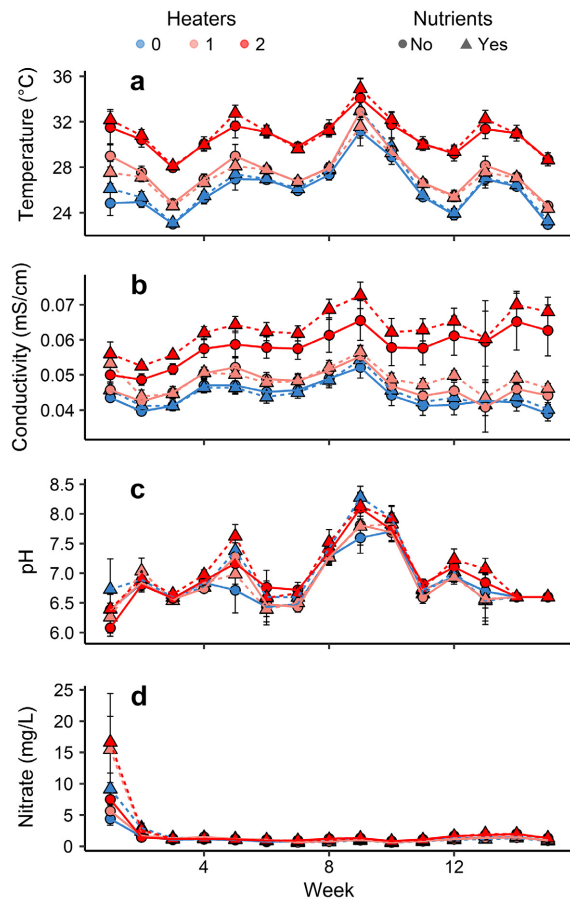


FIG. 1. (a) Temperature, (b) conductivity, (c) pH, and (d) nitrate (mean  $\pm$  SE) in each treatment across the duration of the experiment. Treatments were three levels of heating (0, 1, or 2 heaters per mesocosm) crossed with nutrient reagent addition (No, no nutrients added; Yes, nutrients added). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

S1: Table S1). The abundance of all insects was highest in mesocosms without heaters, declined with additional heaters, and was unaffected by nutrient addition (Table 1, Fig. 2a). Richness positively covaried with insect abundance, but did not vary independently with effects of heaters or nutrient addition (Fig. 2b). Alpha

TABLE 1. *P* values of repeated-measures analyses of the effects of heating and nutrients on environmental variables within mesocosms.

Variable	Heaters	Nutrients	H $\times$ N	Week	H $\times$ W	N $\times$ W	H $\times$ N $\times$ W
Chlorophyll	0.1249	0.3109	0.4206	<b>&lt;0.0001</b>	0.2270	0.1123	<b>0.0060</b>
Conductivity	<b>&lt;0.0001</b>	<i>0.0697</i>	0.3878	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.7323	1.0000
Nitrate	<b>&lt;0.0001</b>	<b>0.0047</b>	0.6009	<b>&lt;0.0001</b>	<i>0.0849</i>	<b>&lt;0.0001</b>	0.9545
pH	<b>0.0007</b>	<b>0.0295</b>	0.2454	<b>&lt;0.0001</b>	0.9548	0.9956	0.9971
Phosphate	<b>0.0076</b>	0.1117	0.8250	<b>0.0105</b>	0.8250	0.5331	0.6019
Temperature	<b>&lt;0.0001</b>	0.5335	0.1472	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.9947	0.3150

Notes: All variables are categorical. H, heaters; N, nutrients; W, week. Boldface type indicates statistical significance ( $P < 0.05$ ) and italic type indicates marginal effects ( $0.05 < P < 0.10$ ). Full results are in Appendix S1: Table S2.

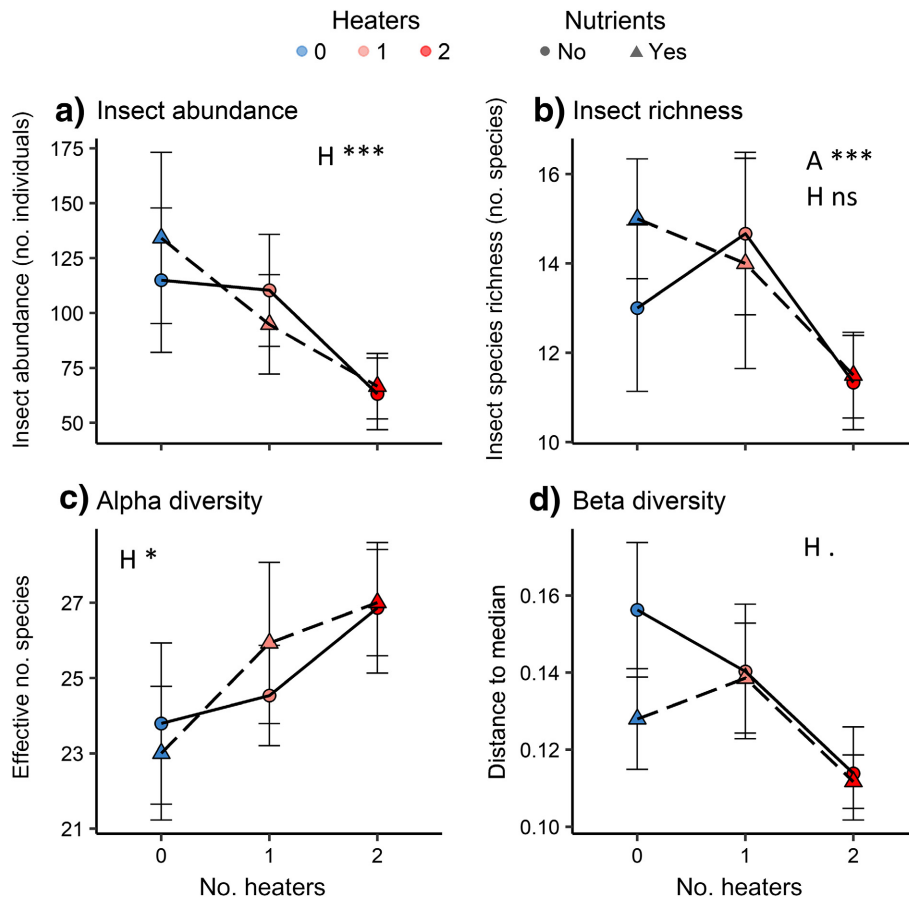


FIG. 2. Values per treatment (mean  $\pm$  SE) across the duration of the experiment for (a) abundance of all insects, (b) species richness of all insects, (c) alpha diversity (Jost's effective number of species), and (d) beta diversity (distance to median). Treatments were three levels of heating (0, 1, or 2 heaters per mesocosm) crossed with nutrient reagent addition (No, no nutrients added; Yes, nutrients added). *Microvelia* were excluded from all analyses. H, heaters; A, abundance of insects; there were no significant effects of nutrients or an interaction with heaters, so these were excluded from figures. Significant effects are indicated by asterisks: \* $0.01 < P < 0.05$ , \*\*\* $P < 0.001$ . Periods indicate marginal effects ( $0.05 < P < 0.10$ ), and ns indicates effects with  $P > 0.10$  (see Table 2 for full results). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

diversity (effective number of species; Jost 2006) increased with the addition of heaters, but was unaffected by nutrient addition (Fig. 2c). Beta diversity marginally declined with the addition of heaters (Fig. 2d), but was unaffected by nutrient addition. There was a significant effect of heaters on assemblage structure (PERMANOVA), but it, too, was unaffected by nutrient addition. The NMDS (Fig. 3a) and shadeplot (Fig. 3b) illustrate the distinct assemblage structures generated by the effect of heaters in our experiment.

Seven of the 43 species/genera were above our threshold for individual analysis (Table 2; Appendix S1; Table S1; Fig. 4). *Copelatus glyphicus* (Fig. 4a) and *Paracymus* (Fig. 4e) had significant effects of heaters, with the highest abundances in mesocosms with no heaters, but had no effects of nutrients or their interaction with temperature. *Microvelia* (Fig. 4d) was the only taxon with a marginal heater  $\times$  nutrient interaction, and they also had a significant effect of heaters, but no main

effects of nutrients. The other four common taxa, *Enochrus ochraceus* (Fig. 4b), *Laccophilus fasciatus* (Fig. 4c), *Peltoodytes sexmaculatus* (Fig. 4f), and *Sigara* (Fig. 4g), had no effects of heaters, nutrients, or their interaction.

## DISCUSSION

As one of the most important environmental factors influencing biology at all scales, temperature is a critical determinant of species distributions and community structure. In a world with changing climate, we must understand not only how rising temperature and its interaction with other environmental factors affect organisms physiologically, but also how organisms behaviorally respond to this variation (Fey et al. 2019). Overall, colonizing aquatic insects responded to variation in patch temperature (via heaters) by selectively colonizing patches with lower temperatures (fewer heaters), but these effects did not interact with nutrient addition

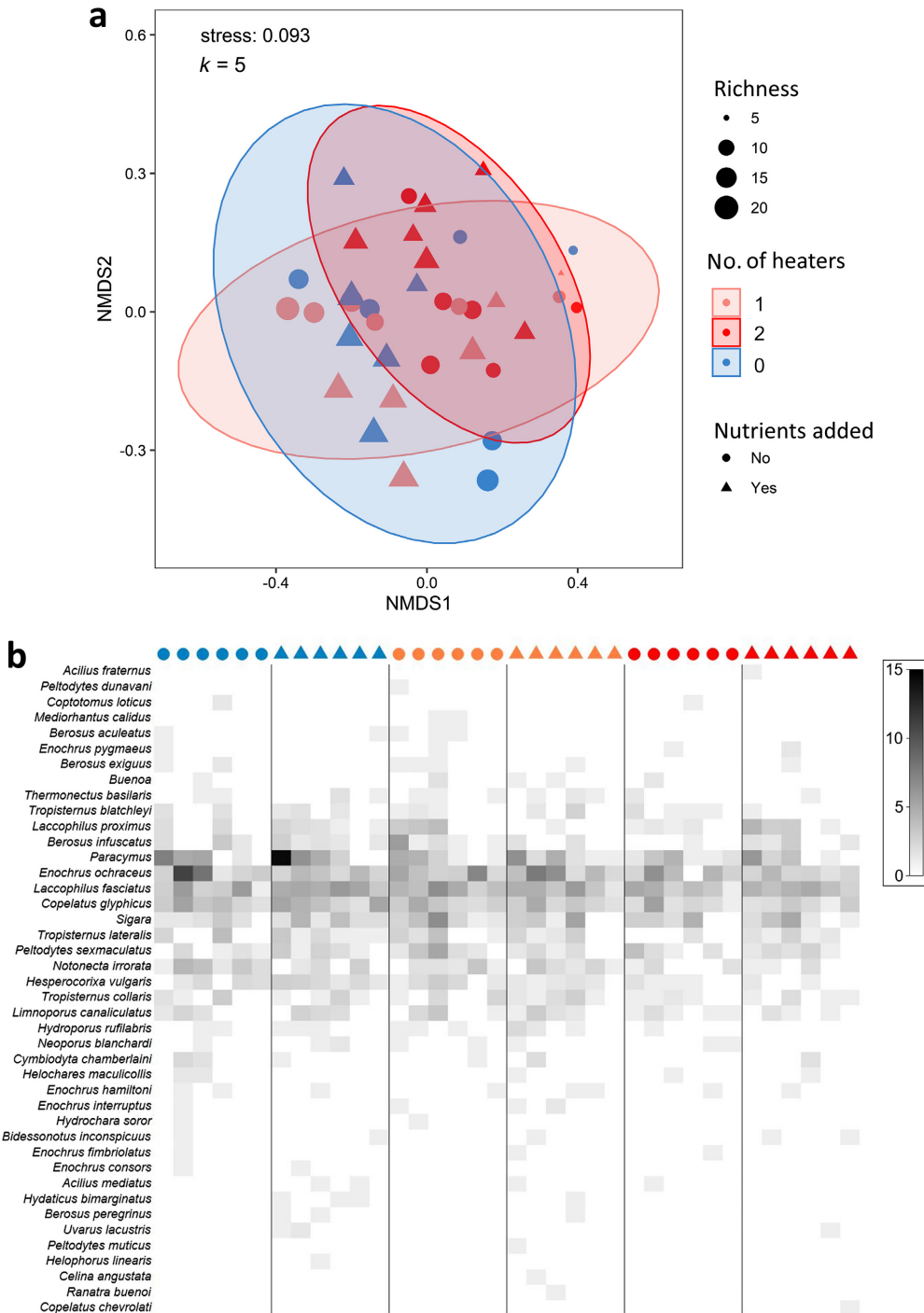


FIG. 3. Illustrations of effects of heaters (0, 1, or 2 per mesocosm) and nutrient reagent addition (No, no nutrients added; Yes, nutrients added) on insect assemblages in the mesocosm experiment. (a) Nonmetric multidimensional scaling (NMDS) plot of the insect assemblage (excluding *Microvelia*) with 95% CI ellipses for effects of heaters, with shapes indicating nutrient addition and point size representing taxonomic richness. Data used for the NMDS plot are scaled within blocks (number per mesocosm/average number per block  $\times$  total number across experiment) and square-root transformed to focus on main effects of heaters and nutrients for illustrative purposes only. (b) Shade plot (heat map) showing square-root transformed abundances for the insect assemblage illustrating assemblage composition in the six treatments (heaters  $\times$  nutrients). Darker colors indicate greater abundance. Treatments ordered by number of heaters, then by nutrients. Species order based on similarity of distribution. Shapes and colors above panel b are the same as in the legend to the right of panel a. See PERMANOVA and beta diversity results (Table 2). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

to shape insect assemblages, and nutrient addition had no independent effects.

Community-level effects were driven by effects on colonization patterns of individual taxa: patch characteristics, as assessed by individual colonists, created the observed patterns of distribution, abundance, and community composition. Overall abundance was lower in heated patches and showed no significant effects of nutrients (Fig. 2), and the taxon-specific colonization patterns combined to result in differing assemblage structures (Fig. 3). Colonization patterns of the seven most abundant species/genera (Fig. 4) varied in taxonomically specific ways, with individual taxa within and across beetle and hemipteran families having no consistent responses. Both hydrophilids (*E. ochraceus*, *Paracymus*) responded differently from one another, as did both dytiscids (*C. glyphicus*, *L. fasciatus*), and both hemipterans (*Microvelia*, *Sigara*). These differences in responses among species/genera within and among families and orders are not surprising, as species-specific colonization patterns are often observed with aquatic insects (Pintar and Resetarits 2017c, Pintar et al. 2018).

The pulse of nutrients added to mesocosms at the start of the experiment (both reagent and leaf litter) appears to have been quickly assimilated, with free nutrients rapidly declining over time (Fig. 1d). Therefore, effects of nutrients on colonization could have occurred through increased primary production throughout the experiment, but our chlorophyll results were inconclusive and likely did not fully capture the amount of primary production. Any effects of nutrients on primary production would also likely affect secondary production, and possibly colonization by predators, but the amount and quick assimilation or mineralization of freely available nutrients appears to not have had effects on colonization by predators. Altogether, our nutrient treatment effectively simulated a single pulse of nutrients, as might occur with initial filling of a temporary pond or runoff following rainfall, but not a habitat with consistently high available nutrient levels.

In contrast to the lack of any effects of nutrients, heaters had stronger effects on both individual taxa and community metrics. The pattern observed for abundance of all insects, *C. glyphicus*, and *Paracymus*, was lower abundances in warmer (heated) patches, with other species trending towards that same pattern (Fig. 4); no species had trends towards higher abundances in heated patches. Many species that did not respond to temperature are known to respond to variation in other patch characteristics, such as leaf litter abundance (Pintar and Resetarits 2017a), leaf litter type (Pintar and Resetarits 2017c), and prey abundance (Pintar and Resetarits 2017b), further building on the array of patch characteristics that generate interspecific variation in responses and drive species sorting. Responses to temperature here are despite the fact that the maximum temperatures recorded in our mesocosms were still below those we have observed in some ponds at UMFS (~40°C), particularly small and

drying ponds in late summer. Indeed, related to this observation, ponds with higher temperatures could also be indicative of ponds with greater risk of desiccation, rather than a response to higher temperatures per se, e.g., near or above thermal tolerances (40°–50°C for most insects, including Dytiscidae; Neven 2000, Calosi et al. 2010). Specific thermal tolerances are not known for any of our species, so it is difficult to have data-based reasons for determining why species responded to temperature. However, while responses to higher desiccation risk are conceivable, specific responses to patch characteristics, such as temperature, should be more relevant to current patch quality.

Temperature has a wide range of effects on ectotherms and can lead to differences in performance and fitness. Thermal tolerances and optimal temperatures vary widely between species (Brown et al. 2004), and top predators are often the first in the community lost as water temperatures increase (Petchev et al. 1999). Water temperature for aquatic ectotherms will ultimately determine individual metabolic and respiration rates, which influence energy and nutrient demand (Gillooly et al. 2002, Brown et al. 2004) and result in variation in growth rate, development, and reproductive and dispersal phenological success rates (Clissold et al. 2013, Abram et al. 2017). Dissolved oxygen is typically lower in warmer aquatic habitats (Moran et al. 2010), but adult beetles and hemipterans can breathe atmospheric oxygen. This enables survival in warm or eutrophic conditions, with organisms returning to the water surface if additional oxygen is needed, although air-breathing species can also be sensitive to dissolved oxygen (Silberbush et al. 2015). While specific mechanisms of respiration vary among species and life stage, higher temperatures may also increase frequency of return to the water surface (Verberk et al. 2005, 2020) and in turn shape behavior and community interactions.

Many predatory gilled organisms (particularly fish, but also others like larval salamanders and odonates) may not be able to survive in warmer habitats since they rely on sufficient dissolved oxygen in the water column for respiration. Hence, warmer habitats may, from one perspective, be higher quality habitats for adult beetles because of lower predation risk and higher reward (nutrients), but we observed the opposite: higher abundances when temperatures were lower (fewer heaters). Many colonizing aquatic insects can detect and avoid fish, so temperature need not serve as a surrogate for fish presence (Resetarits and Pintar 2016, Resetarits et al. 2019). Avoidance of higher temperatures could be due to negative effects of temperature on metabolism and respiration, as temperatures near upper thermal limits lead to a range of physiological damages (Neven 2000, Calosi et al. 2010). Similarly, higher resource requirements due to higher metabolic rate may not be met in warmer habitats. Habitat preferences among aquatic insects may also be geared to better match offspring performance than that of adults; although it can vary, larvae are usually

TABLE 2. Results of analyses of the effects of heaters, nutrient addition, and their interaction on abundance of all insects, taxonomic richness, alpha diversity, assemblage structure, beta diversity, and abundances of common taxa ( $N > 125$ ) in mesocosms.

Effect	SS	MS	Numerator df	Denominator df	<i>F</i>	<i>P</i>	<i>P</i> (BH)	$\eta_p^2$
Insect abundance (3505)								
Heaters	50.94	25.47	2	30	9.188	<b>0.0008</b>	<b>0.0064</b>	0.376
Nutrients	0.06	2.62	1	30	0.023	0.8800	0.9161	0.001
H × N	5.24	2.62	2	30	0.946	0.3996	0.5328	0.058
Insect richness								
Abundance	2.78	2.78	1	13.1	37.741	<b>&lt;0.0001</b>		0.538
Heaters	0.13	0.07	2	30.5	0.902	0.4164		0.053
Nutrients	0.03	0.03	1	25.4	0.365	0.5510		0.011
H × N	0.07	0.03	2	26.1	0.441	0.6480		0.026
Alpha diversity (Jost's effective number of species)								
Heaters	75.11	37.56	2	30	5.305	<b>0.0107</b>		0.257
Nutrients	0.56	0.56	1	30	0.079	0.7810		0.003
H × N	7.18	3.59	2	30	0.507	0.6072		0.032
Assemblage structure (PERMANOVA)								
Heaters	0.054	0.027	2	30	1.216	<b>0.0241</b>		0.075
Nutrients	0.010	0.010	1	30	0.451	0.6797		0.015
H × N	0.035	0.018	2	30	0.801	0.2246		0.051
Beta diversity (distance to median)								
Heaters	0.006	0.003	2	33	2.825	<i>0.0737</i>		0.146
Nutrients	0.001	0.001	1	34	0.416	0.5234		0.012
<i>Copelatus glyphicus</i> (369)								
Heaters	8.17	4.08	2	30	5.496	<b>0.0093</b>	<b>0.0372</b>	0.260
Nutrients	0.01	0.01	1	30	0.011	0.9161	0.9161	0.000
H × N	0.92	0.46	2	30	0.622	0.5438	0.5798	0.038
<i>Enochrus ochraceus</i> (666)								
Heaters	8.50	4.25	2	30	1.723	0.1957	0.3131	0.099
Nutrients	3.64	3.64	1	30	1.478	0.2337	0.4674	0.045
H × N	6.83	3.42	2	30	1.386	0.2657	0.4586	0.081
<i>Laccophilus fasciatus</i> (642)								
Heaters	1.559	0.780	2	30	0.767	0.4732	0.6218	0.047
Nutrients	1.90	1.90	1	30	1.873	0.1813	0.4674	0.056
H × N	4.47	2.24	2	30	2.200	0.1284	0.3424	0.123
<i>Microvelia</i> (665)								
Heaters	15.12	7.56	2	30	3.388	<b>0.0471</b>	<i>0.0942</i>	0.122
Nutrients	4.64	4.64	1	30	2.079	0.1597	0.4674	0.024
H × N	13.73	6.86	2	30	3.076	<i>0.0610</i>	0.3424	0.099
<i>Paracymus</i> (608)								
Heaters	22.35	11.18	2	30	4.051	<b>0.0277</b>	<i>0.0739</i>	0.209
Nutrients	4.51	4.51	1	30	1.635	0.2108	0.4674	0.051
H × N	3.06	1.53	2	30	0.555	0.5798	0.5798	0.035
<i>Peltodytes sexmaculatus</i> (130)								
Heaters	0.72	0.36	2	30	0.483	0.6218	0.6218	0.029
Nutrients	0.23	0.23	1	30	0.312	0.5805	0.9161	0.009
H × N	3.47	1.73	2	30	2.330	0.1147	0.3424	0.124
<i>Sigara</i> (273)								
Heaters	1.49	0.75	2	30	0.555	0.5797	0.6218	0.034
Nutrients	0.05	0.05	1	30	0.034	0.8549	0.9161	0.001
H × N	3.50	1.75	2	30	1.303	0.2866	0.4586	0.076

Notes: Overall insect abundance was included as a covariate in the richness analysis. Boldface type indicates statistically significant *P* values ( $P < 0.05$ ) and italic type indicates marginal effects ( $0.05 < P < 0.10$ ). *P* (BH) are *P* values for abundances adjusted for the false discovery rate via the Benjamini and Hochberg (1995) procedure.  $\eta_p^2$  is an estimate of effect size. Numbers in parentheses indicate abundances of that taxon (see Appendix S1: Table S1). *Microvelia* were excluded from all analyses except their own.

found in the same microhabitat type as the adults of that species (Fairchild et al. 2003). Therefore, colonization decisions are a balance of risk and reward for both adults and larval offspring.

Our results indicate colonizing aquatic insects may be able to mediate negative effects of rising water temperatures by choosing habitats with lower temperatures. Long term, increasing water temperatures can have



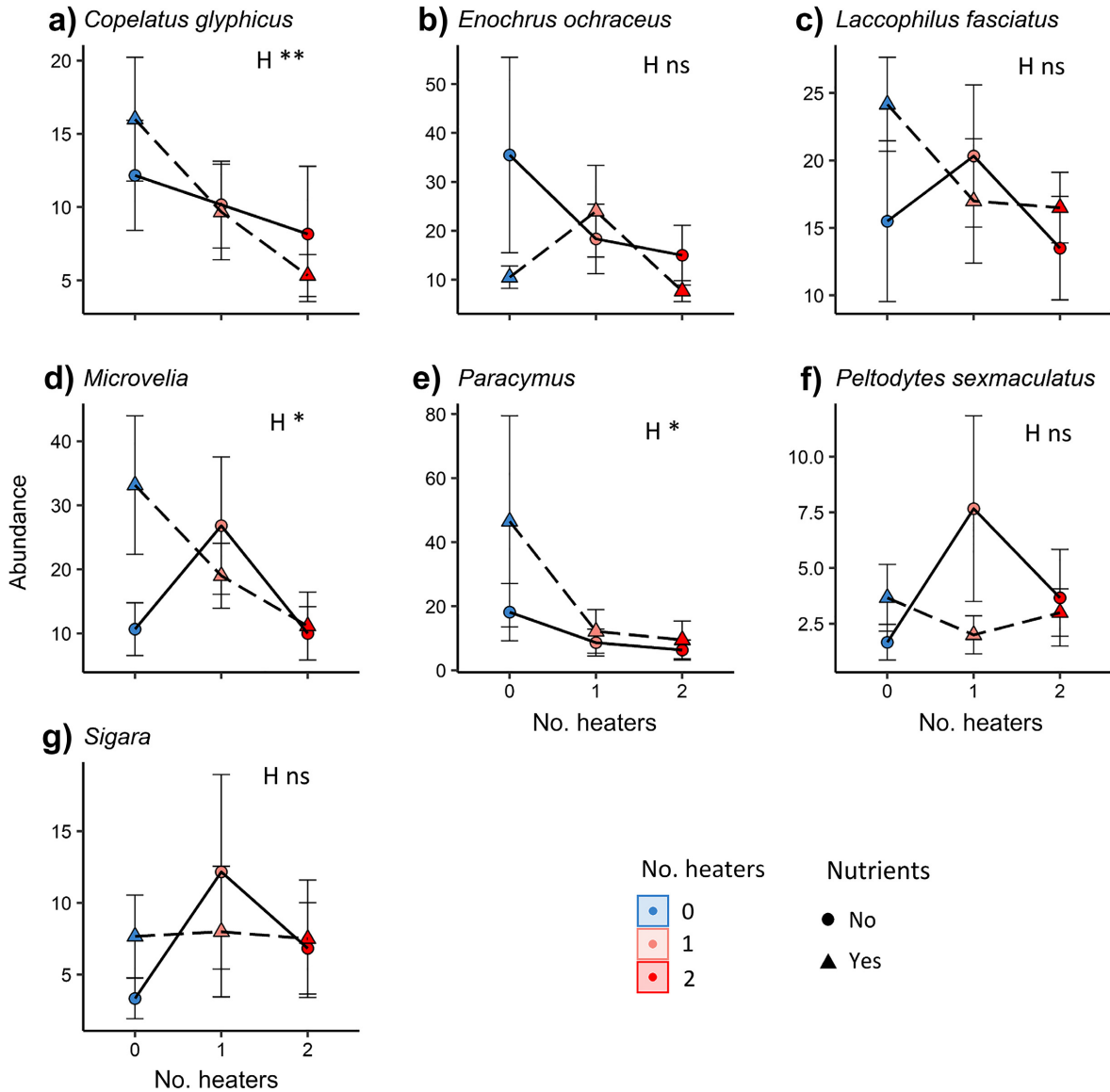


FIG. 4. Cumulative abundances per treatment (heaters × nutrients; mean ± SE) across the duration of the mesocosm experiment for common species/genera ( $N > 125$ ) listed alphabetically. H, heaters (0, 1, or 2 heaters per mesocosm); there were no significant effects of nutrients or an interaction with heaters, so these were excluded from figures. Significant effects are indicated by asterisks: \* $0.01 < P < 0.05$ , \*\* $0.001 < P < 0.01$ ; ns indicates effects with  $P > 0.10$  (see Table 2 for full results). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

impacts on the macroinvertebrate species composition within lentic habitats (Burgmer et al. 2007). Species with the lowest tolerance to higher temperatures will be the most vulnerable because they will have the least ability to acclimate (Calosi et al. 2008). Species that are less adapted to warmer temperatures may incur an increase in the cost of thermoregulation because they will need to disperse to find a more suitable habitat, if possible, which can be energetically expensive and increases the risk of predation and dehydration (Dudley 2002, Fey et al. 2019). Many adult aquatic beetles have limited secondary dispersal abilities and a possible oogenesis-flight

syndrome, where the tradeoff of keeping flight muscles can stop the development of ovaries or result in lower fecundity, increasing the importance of initially colonizing a habitat patch of high quality (Bilton et al. 2001).

However, the ability to mediate negative effects of warmer water through habitat selection may result in more complex interactions with other species and habitat types across a landscape (Amundrud and Srivastava 2019). In a scenario where changing environmental conditions increase patch temperature above the optimum for thermally sensitive species, greater colonization rates in cooler patches leads to increased density. This results

in the compression of more individuals of more species into cooler patches, thus, habitat selection may exacerbate effects of rising temperatures if suitable patches are limiting and there is greater competition (and predation) within those patches. If intra- or interspecific density-dependence plays a role in habitat selection, spatial compromise may occur, leading to more colonists in suboptimal patches than would be expected (Resetarits et al. 2005). Similarly, if temperatures in the coolest patches become very warm and unfavorable, habitat selection across a temperature gradient may become a less important patch characteristic for colonists, as all patches may be of low quality. Thus, while habitat selection may allow species to respond adaptively to increasing temperatures, the resulting scenarios are far from simple when considered at the landscape scale and suggest that habitat shifts, like range shifts, can have cascading effects (Resetarits et al. 2005, Crowley et al. 2019).

Cooler patches must be available for habitat selection to be an effective response. While on some landscapes, like UMFS, there are wide arrays of thermal differences across freshwater habitat patches, many of the coolest patches are permanent, spring-fed, and contain fish. This creates a scenario where colonists must balance relative risks and benefits of both cool and warm patches. Primary habitat selection is clearly responsive to temperature differences and results in distinct assemblages of insect colonists arriving in patches. How post-colonization processes affect individuals in a patch, and what the resulting insect assemblages look like, remain to be determined, but colonization dynamics clearly set the stage for any later interactions.

Aquatic insects are able to thrive in a wide variety of habitat types, from permanent and temporary ponds, to streams, rivers, and springs, all of which are impacted differently by environmental and anthropogenic stressors. Variation in abiotic and biotic conditions such as water temperature and nutrient enrichment within and among habitats may affect the colonization of aquatic insects, as differences in thermal plasticity and desiccation resistance between species may be important factors in determining where individuals occur (Gaston and Chown 1999, Fairchild et al. 2003, Verberk et al. 2005, Calosi et al. 2010, Chown et al. 2011). Because many aquatic invertebrates are sensitive to environmental conditions in aquatic systems, and since abundance and diversity are directly related to conditions in a habitat, aquatic invertebrates are important bioindicators that reflect changes in habitat quality (Mazor et al. 2006, Wahizatul et al. 2011).

On a warming Earth, whether organisms have the plasticity to respond to increasing temperatures will play a vital role in determining the distribution of organisms. Habitat selection is a key component of the biology of most animals, regardless of habitat. To understand biodiversity change with increasing temperature, we must link behavioral responses like habitat selection with developmental responses, species interactions, and

changes in other environmental conditions. We observed that colonizing aquatic insects not only responded to temperature treatments (heaters), but selected patches with lower temperatures (fewer heaters), and that these habitat preferences led to distinct assemblages across patches based on temperature. Thus, some species can potentially mediate proximal negative effects of warming through behavioral responses, but the effectiveness of that strategy depends on the availability and distribution of remaining suitable habitat. Any reduction in suitable habitat, via whatever mechanism, has the potential to constrain distribution and abundance, and hence local and regional diversity. Thus, habitat selection responses to warming may alter population and community dynamics, with concomitant impacts across ecosystems.

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## DATA AVAILABILITY STATEMENT

Associated data are available on Figshare: <https://doi.org/10.6084/m9.figshare.12728702>