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Thermal sensitivity modulates temporal patterns of ecosystem functioning by freshwater mussels

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Abstract

1. The continued global loss of biodiversity highlights the importance of understanding how species loss may impact ecosystem function. Shifting temperatures will accelerate species loss, but will affect species differently.
2. We investigated effects of temperature (10°C, 20°C, or 30°C) on resource acquisition and assimilation (clearance rate, respiration rate, N and P excretion) for 11 freshwater mussel species from a species-rich assemblage in the Sipsey River, Alabama, U.S.A., to evaluate how temperatures impact co-occurring species and the ecosystem processes they facilitate. Mussels are assigned to the same guild (i.e., filter-feeding bivalves), but span a breadth of evolutionary lineages and have a diversity of life history strategies from short-lived, quickly maturing species to long-lived, slow-growing species.
3. Our results indicated that four species (*Cyclonaias asperata*, *Elliptio arca*, *Lampsilis ornata*, and *Obovaria unicolor*) were thermally sensitive at 30°C, using more energy than they were acquiring. These species spanned three phylogenetic tribes and two different life-history strategies suggesting thermal tolerance may not necessarily be linked to life history strategy or phylogenetic constraints.
4. When laboratory clearance and excretion rates were scaled to a natural mussel community over a year, we found that relative contributions by the proportion of thermally tolerant and sensitive species to total ecosystem function varied temporally across temperature and flow regimes. Thermal stress enhanced contributions by sensitive species' during summer, as individuals attempted to meet metabolic demands by increasing clearance rates and use of energy stores that increased ammonia excretion. River discharge and background nutrient concentrations also modulated the impact of ecosystem functioning facilitated by mussels. High river discharge in winter and high background nutrient concentrations in the summer decreased the relative contribution of the mussel community.
5. Although mussel species are commonly grouped in a single guild, species-specific thermal traits modulate their role in the community. As biodiversity decreases, even biomass replacement by surviving mussel species is unlikely to support comparable ecosystem function due to the loss of unique species traits.

KEYWORDS
biodiversity, clearance rate, filtration rate, nutrient excretion, thermal tolerance

1 | INTRODUCTION

The reverberations of climate change are resulting in altered ecosystem processes and structure and affecting ecosystem services in freshwater systems worldwide (Allison et al., 2009; Grimm et al., 2013; Woodward et al., 2010). While predicted changes in climate patterns are inconsistent across regions, many areas are anticipated to have increased drought intensity and frequency due to altered patterns in precipitation, evapotranspiration, and increased human demand (Baron et al., 2002; Dai, 2013; Trenberth et al., 2014). Under these conditions, perennial streams may experience low or intermittent flow, subjecting stream ecosystems to elevated temperatures (Atkinson et al., 2014; Mosely, 2015). Thus, there is a need to understand organismal responses to thermal variation as climate change acts as a selective pressure on organismal physiological tolerance, species distributions, and ecosystem processes (Angilletta & Angilletta, 2009; Bush et al., 2016; Rohr et al., 2018).

Animal consumers are an integral component of biogeochemical processes and ecosystem function (Atkinson et al., 2017; Elser et al., 2000; Shurin et al., 2012; Vanni, 2002). Feeding activities by consumers exert top-down control by limiting biomass of lower trophic levels, and bottom-up control of elements previously bound in prey tissue via egestion and excretion are recycled (Power, 1990; Schmitz et al., 2010; Vanni et al., 2013). In freshwater systems, limited animal movements and stressful high temperature events resulting from low discharge during extreme climatic events could eventually shift community composition to more thermally tolerant species through sensitive species loss (DuBose et al., 2019; Hopper et al., 2020). Globally, freshwater ecosystems are expected to suffer from more frequent and more intense periods of drought and continued loss of natural land cover, exasperating stress to aquatic organisms (DuBose et al., 2019; Martinuzzi et al., 2014; Poff et al., 2012).

Organismal contributions to ecosystems are dependent on their functional traits, which emerge from phenotypic characteristics related to growth, reproduction, and survival (Violle et al., 2007). Functional traits can modulate prey selection, feeding rates, and nutrient provisioning quantity and quality (Atkinson & Vaughn, 2015; Baker & Levinton, 2003; Vaughn et al., 2004). Metabolism, as linked to body size (i.e., smaller individuals have higher mass-specific metabolic rates) and species-specific functional traits, intricately control feeding, respiration, egestion, and excretion rates across species (Brown et al., 2004; Daufresne et al., 2009). The diversity of organismal functional traits is constrained by the environment (Tilman, 2001; Violle et al., 2007) and responses to specific environmental stressors are often not well described (Díaz et al., 2013).

Abiotic factors (e.g., nutrient concentration, discharge, and temperature) can modulate the expression of species traits related to physiology, thus altering their contributions to ecosystem function (Benstead et al., 2010; McIntyre et al., 2008). In systems with high anthropogenic nutrient loading, consumer contributions often have diminished impacts particularly when biomass is low (Capps et al., 2015; Spooner et al., 2013; Wilson & Xenopoulos, 2011). High flow events enhance ecosystem size, overwhelming the contribution of consumers, thus resulting in consumers having a lower relative contribution to energy and nutrient fluxes (Atkinson & Vaughn, 2015; Vaughn et al., 2004). At lower temperatures ectotherms have slower metabolic rates resulting in lowering consumer contributions (Allen & Gillooly, 2009; Gillooly et al., 2001). Higher temperatures may force consumers beyond their thermal limit, altering ecosystem source/sink dynamics (DuBose et al., 2019). During periods of growth, consumers act as net nutrient sinks, but thermal stress can induce usage of energy stores, decreasing body condition and causing a shift to a net nutrient source (Spooner & Vaughn, 2008). While the effects of temperature on trait expression have been documented, temperature induced changes in consumer contributions to ecosystem function remain poorly understood. Ultimately, temperature is an important selective agent for physiological and ecological traits, thus providing a basis for understanding patterns of stream biodiversity and ecosystem function.

Here we studied variation in thermal traits of freshwater mussels (Bivalvia: Unionidae), hereafter mussels, a diverse guild of long-lived (~3–100 years) filter-feeding benthic bivalves (Haag, 2012). Occurring in dense speciose aggregations (mussel beds), mussels serve as a strong link between pelagic and benthic habitats transferring suspended material to the benthos and releasing dissolved material to the water column (Vaughn, 2018; Williams et al., 1993). While mussels are assigned to the same general guild (i.e., filter-feeding bivalves), they have a diversity of life history strategies that span short-lived, quickly maturing species (e.g., opportunistic) to long-lived, slow-growing species (e.g., equilibrium) (Haag, 2012; Moore et al., 2021) and span a breadth of evolutionary lineages (Pfeiffer et al., 2019). Mussel communities are currently experiencing dramatic declines in both diversity and abundance, highlighting the need to better understand how their losses and change in community composition may impact ecosystem function (Lopes-Lima et al., 2018). As ectotherms, mussel physiological processes are directly controlled by ambient water temperature, and previous studies have demonstrated differing patterns in metabolism across temperatures (Clarke & Johnston, 1999; Hill & Magnuson, 1990; Vanni & McIntyre, 2016). Consequently, as species approach their thermal maximum, they may be extirpated from the system resulting community shifts and long-term loss of their contributions to ecosystem processes (DuBose et al., 2019; Huss et al., 2019; Spooner & Vaughn, 2008).

Given the coupled concern of the imperilled status of freshwater mussels and anticipated changes to stream temperatures, our goal

was to test temperature effects on physiological performance across co-occurring mussel species to better understand thermal sensitivity. Additionally, we used these data to understand the interaction between temperature and biodiversity on mussel-provided stream ecosystem functions. We measured three ecologically relevant physiological rates (i.e., clearance, respiration, and excretion rates) in 11 species of mussels across three temperatures (10°C, 20°C, or 30°C) to examine: (1) How do physiological rates vary with temperature and species? (2) Which species are most sensitive to warm water temperatures and does that correspond to life history strategy or phylogenetic grouping? (3) Do species with different thermal preferences contribute differentially to ecosystem functioning across an annual cycle? We predicted that physiology would govern the overall performance under the thermal treatments and that the expression of species traits may be linked to specific life history strategies and/or phylogenetic grouping. Specifically, species that are better suited to recover faster (i.e., resilient opportunistic and periodic strategists that are shorter-lived with high fecundity) may be more thermally sensitive while species that are more resistant to thermal stress may be slower growing and later maturing taxa (i.e., equilibrium species). As these life history traits are often phylogenetically conserved, we anticipated thermal traits may also be linked to phylogenetic history. Lastly, we predicted that the contributed ecological functions of the total mussel community to the ecosystem would vary temporally in response to temperature across the year due to trait-dependent thermal preferences.

2 | METHODS

2.1 | Collection and acclimation

We collected mussels from the Sipsey River, Greene County, Alabama, U.S.A. The Sipsey River is a fifth-order alluvial river, draining 2,044 km^2 with extensive forested floodplain wetlands, flowing primarily through the Eastern Gulf Coastal Plain physiographic province (McGregor & O'Neil, 1992). Due to relatively low levels of human modification the Sipsey River supports one of the most intact and diverse biological communities in the region, including most of its historical native mussel fauna (Haag & Warren, 2010; Hopper et al., 2012).

We collected 30 individuals, when possible, each of *Cyclonaias asperata*, *Fusconaia cerina*, *Lampsilis ornata*, and *Obovaria unicolor* in July–September of 2017, and *Amblema plicata*, *Elliptio arca*, *Elliptio crassidens*, *Obliquaria reflexa*, *Pleurobema decisum*, *Quadrula rumphiana*, and *Tritogonia verrucosa* in July–October of 2018 (sensu Williams et al., 2017 nomenclature). These unionid species span four distinct phylogenetic tribes within a single subfamily (Ambleminae) and express different life-history strategies (Table 1). Mussels were transported to the Ecological Wet Laboratory at the University of Alabama, Tuscaloosa, Alabama, U.S.A. and held in three separate Frigid Units Living Streams outfitted with recirculating chillers (Toledo, OH) and Process Technology immersion heaters (Willoughby, OH). Water temperature was held at river temperature (19–23°C) on the day of collection and mussels were held at this temperature for 1 week post collection to recover from transportation and handling stress. Living Streams contained trays of Sipsey River sediment to allow for burying and reduce stress on individuals during acclimation. We fed the mussels an algal culture (primarily a mix of green algae and diatoms) from the Black Warrior River, Alabama daily. Partial water changes were conducted every three days.

After the initial 7-day period, acclimation to experimental temperatures (10°C, 20°C, or 30°C) began. These temperatures were selected as they represent an annual range experienced in the Sipsey River (Atkinson et al., 2019). Temperatures in Living Streams were changed by up to 1°C/day, and timed so all mussels reached their experimental temperature on the same day. Two days before physiology trials, no algae culture was added, and a 50% water change was completed to deplete food in the tanks and allow individuals to clear remaining forage from their guts. On the day prior to experimentation, all individuals were measured for shell length (mm) and wet weight (g), scrubbed of biofilm, and individually tagged. On the day of the trial, individuals were lightly scrubbed, rinsed, and placed directly into individual 1-L plastic test chambers. Chambers were held at experimental temperatures inside incubators (Percival Scientific, Perry, Iowa). Individual chambers were equipped with stir bars to ensure even mixing during the monitoring period. Mussels rested on a mesh surface suspended above the stir bar in the test chambers to reduce disturbance.

2.2 | Clearance rate determination

One-litre test plastic test chambers were used and filled with 750 ml of filtered stream water, and a 50-ml aliquot of algal solution to achieve a minimum 50 mg chlorophyll-*a*/L within the chamber. A 50-ml sample was taken from each chamber at start the trial and individual exposure times varied for 0.5–3 hr depending on individual mussel size and temperature treatment with incubations at lower temperatures and with smaller individuals lasting longer. A second 50-ml sample was taken at the end of the trial. Water samples were filtered onto pre-ashed 25-mm glass-fibre filters (pore size = 0.7 μm; MilliporeSigma, Burlington, MA) and immediately frozen until extraction. Following a 12-hr acetone extraction using standard methods (Wetzel & Likens, 2013), samples were analysed on a UV–Vis spectrophotometer (Genesys 10S, Thermo Scientific). From these two measurements a mass-adjusted clearance rate was calculated as:

$$CR = V \ln\left(conc_i / conc_f\right)(M\,t)$$

CR is clearance rate (volume filtered g dry tissue $weight^{-1}$ hr^{-1}), V is volume (L), $conc_i$ is initial chlorophyll-*a* concentration (mg/L), $conc_f$ final chlorophyll-*a* concentration (mg/L), M is dry tissue mass (g), and t is time (h). Control chambers ($n = 5$, per experimental temperature) without mussels were used to determine and adjust for settling rate.

TABLE 1 Dry tissue mass (g) range for test species evaluated in this study, phylogenetic tribe grouping (Pfeiffer et al., 2019), and their life history strategy (Haag, 2012; Moore et al., 2021)

				Acquisition	Assimilation		Ecological Functions		Thermal Group
Species	**Phylogenetic tribe**	**Life history strategy**	**Dry mass (g)**	**Clearance rate**	**O_2 consumption**	**Δq_{10}**	**Nh_3 excretion**	**P excretion**	**Thermal tolerance**
Amblema plicata	Amblemini	Equilibrium	1.2–6.0	+	=	A>C	=	–	Tolerant
Lampsilis ornata	Lampsilini	Periodic/ Opportunistic	0.4–6.7	=	+	A<C	+	=	Sensitive
Obliquaria reflexa	Lampsilini	Periodic	0.2–2.1	=	+	A>C	=	=	Tolerant
Obovaria unicolor	Lampsilini	Periodic	0.1–1.4	=	=	A<C	=	=	Sensitive
Elliptio arca	Pleurobemini	Periodic	0.6–2.3	+	+	A<C	+	=	Sensitive
Elliptio crassidens	Pleurobemini	Equilibrium	2.1–7.0	+	+	A>C	=	=	Tolerant
Fusconaia cerina	Pleurobemini	Equilibrium	0.2–1.7	=	=	A>C	=	=	Tolerant
Pleurobema decisum	Pleurobemini	Equilibrium	0.3–1.0	+	+	A>C	=	=	Tolerant
Cyclonaias asperata	Quadrulini	Equilibrium	0.2–1.6	+	=	A<C	+	=	Sensitive
Quadrula rumphiana	Quadrulini	Equilibrium	0.8–3.7	=	+	A>C	=	=	Tolerant
Tritogonia verrucosa	Quadrulini	Equilibrium	0.9–3.8	+	+	A>C	=	–	Tolerant

Note: Opportunistic mussels have high growth rates, are short-lived, mature quickly, and have a moderate to large body size. Periodic species have a moderate life span, a low to moderate age at maturity, and a small to moderate body size. Equilibrium species tend to have longer life spans, mature slowly and have a moderate to large body size. Functional response (ΔQ_{10}) to experimental temperatures between 20 and 30°C. A<C represents a shift to anabolism < catabolism, A>C represents anabolism > catabolism. + and – indicate a significant ($p<0.05$) positive and negative difference in rate means determined by ANOVA with a Tukey's post hoc test, and = indicates no significant difference.

2.3 | Respiration and excretion determination

Following clearance rate measurements, individuals were rinsed in filtered water, and placed in a second test chamber. Chambers were filled with filtered stream water until all air bubbles were removed. Initial O_2 concentrations were measured using a YSI ProODO (Yellow Springs, OH) and the chambers were sealed. Chambers incubated for 0.5–3 hr depending on individual mussel size and temperature treatment similar as above to prevent dissolved oxygen from going below 5 mg/L. Chambers were unsealed and a final O_2 concentration recorded. Chamber water was filtered through an ashed 47-mm glass fibre filter (pore size = 0.7 μm; MilliporeSigma), and final water volume was measured with a graduated cylinder. Filtrate was collected and analysed for ammonia (N) and orthophosphate (P) using a Lachat Quickchem FIA+8,000 Series flow injection analyser (Hach Company) and used to calculate biomass adjusted excretion rates. Controls were used to adjust for background changes in O_2, and as the starting nutrient concentration. Following the experiments, soft tissue was separated from the shell and dried and weighed for dry-mass determination with the exception of *Pleurobema decisium* (dry mass was estimated using length-dry mass conversions from Atkinson, Parr, et al., 2020) as it is a federally endangered species. Mass-specific respiration rates were calculated as change in O_2 concentration per hour corrected for water volume, mussel dry tissue mass, and oxygen concentration changes in the control chambers (mol O_2 g^{-1} dry tissue hr^{-1}). N and P excretion rates were calculated as the difference in treatment and control nutrient concentrations (μmol nutrient), then corrected for incubation time (hr) and mass (g). Excretion stoichiometry was calculated as the average N:P (molar) within a species and temperature, to determine N:P molar ratio. All rate data were square-root transformed prior to analysis. We used a one-way ANOVA followed by a Tukey's post hoc test to investigate the effects of temperature within a single species and rate (Table 1; Table S1). A two-way ANOVA was used to examine the relative effects of species, temperature, and species × temperature on physiological rates.

2.4 | Thermal sensitivity

We compared oxygen (O) consumption from respiration and N excretion to assess the relative utilisation of protein in metabolism across experimental temperatures. Lower O:N indicates greater catabolism of protein as an energy source compared to anabolism of carbohydrates and lipids. A greater relative rate of catabolism to anabolism being indicative of thermal stress (Bayne et al., 1985; Widdows, 1978). Q_{10} values quantify the relative change in reaction rates between temperatures differing by 10°C. We calculated the deviation in the anabolism: catabolism between our experimental temperatures as:

$$delta\ Q_{10} = \frac{O_f}{O_i} - \frac{N_f}{N_i}$$

With O_f as the respiration rate at the higher temperature, O_i as the respiration rate at the lower temperature, N_f as the N excretion rate at the higher temperature, N_i as the N excretion rate at the lower temperature, and delta Q_{10} being the change in the relative rate of anabolism to catabolism over a 10°C change in temperature. This was calculated between 10 and 20°C, and between 20 and 30°C, respectively. Since different individuals were used for each treatment, it was not possible to calculate Q_{10} values on the same individuals. Therefore, mean oxygen and ammonia excretion values for each treatment and each species were used to calculate Q_{10} rates. Species with a net shift to catabolism at the peak experimental temperature were classified as sensitive, as they were shifting to energy usage exceeding resource acquisition and depleting energetic stores (Baker & Hornbach, 2001; Spooner & Vaughn, 2008). Species classified as thermally tolerant are still assimilating energy (anabolism > catabolism) at the peak temperature (Spooner & Vaughn, 2008).

2.5 | Scaling to the ecosystem

Species physiological rates obtained in trials were scaled to a natural mussel bed to assess ecosystem functions provided by freshwater mussels across thermal regimes. The freshwater mussel community was quantitatively surveyed in September 2016 along a 60-m reach of the Sipsey River, AL, and paired with long-term discharge, temperature, and water chemistry data (Atkinson et al., 2019). The 60-m reach was broken into 20-m sections, each with three random transects running perpendicular to flow. Along each transect, 0.25-m^2 quadrats were dug every 1.5 m and sieved. All mussels found were identified to species and measured for length to estimate dry tissue mass using species-specific length–mass equations (Atkinson, Parr, et al., 2020) in order to estimate reach-scale areal biomass (g mussel/m^2). Using our species-specific clearance and excretion rates, we estimated areal rates (L m^{-2} hr^{-1}; μmol nutrient m^{-2} hr^{-1}) as the product of population biomass and per capita rates within the reach based on our measured rates.

We deployed a temperature and pressure transducer at our site and measured discharge when it was possible resulting in 10 discharge measurements at each site to develop a rating curve between depth and discharge over our study period (see Atkinson et al., 2019). Discharge was measured by selecting a straight and uniform section of the stream, and we measured depth and velocity (m/s) every 0.5 m using a Hach FH950 flow meter (Hach Company). Hydrologic residence time (min) was calculated at our experimental temperatures (±2°C), using mean reach volume and velocity (Atkinson et al., 2019). Mean discharge and nutrient concentrations for our experimental temperatures were calculated from measurements taken at experimental temperature (±2°C). Hydrologic residence time (min) was compared to clearance time (reach volume [ml]/total community clearance rate [ml/hr]) to gauge relative impact of community clearance rate on water turnover. To compare contribution of mussel excretion (E_A; μmol

nutrient m^{-2} hr^{-1}) to background nutrient concentrations, we calculated volumetric excretion (E_v; μmol nutrient/L) and turnover distance (McIntyre et al., 2008) as:

$$E_V = \frac{(E_A \times A \times T)}{V}$$

Volumetric excretion integrates area (*A*: length [m] × width [m]), travel time (*T*: length [m] × water velocity [m/s]), and volume (*V*: length [m] × cross-sectional area [m^2]) of the study reach, calculating average addition of dissolved nutrients by the mussel community as water passes through the reach. Turnover distance was calculated as distance of the reach required where volumetric excretion equalled background nutrient concentration, assuming complete mixing and no nutrient uptake.

3 | RESULTS

3.1 | Clearance rates

Mass-corrected clearance rates varied significantly across temperatures and species, but temperature accounted for the greatest variation in observed clearance rates (Figure 1a, Figure S1; Temperature $F_{(2,290)} = 94.524$, $p < 0.001$; Species $F_{(10,290)} = 12.532$, $p < 0.001$). The interaction between temperature and species was also significant ($F_{[20,290]} = 2.887$, $p = 0.002$) demonstrating a variable response to temperature across species. Our post hoc tests indicated that *A. plicata*, *C. asperata*, *E. arca*, and *P. decisum* increased their clearance rates between 20 and 30°C. *Lampsilis ornata*, *O. reflexa*, *and Q. rumphiana* had increased clearance rates only between 10 and 20°C. *Elliptio crassidens and T. verrucosa* had increased clearance rates across all temperatures, while *F. cerina and O. unicolor* were constant across all temperatures (Table. 1; Figure 1a, Figure S1).

3.2 | Respiration rates

Mass-corrected respiration rates varied significantly across temperature and generally increased with temperature (Figure 1b; $F_{(2,290)} = 149.946$, $p < 0.001$). Species ($F_{(10,290)} = 5.651$, $p < 0.001$) and the interaction between temperature and species ($F_{[20,290]} = 4.364$, $p < 0.001$) were also significant. Respiration increased across all temperatures in *E. arca*, *E. crassidens*, *O. reflexa*, *P. decisum*, *Q. rumphiana*, and *T. verrucosa*. An increase in respiration only occurred between 10 and 20°C for *A. plicata* and *C. asperata*. *Fusconaia cerina* respiration rates were constant across temperature, and *L. ornata* only increased between 20 and 30°C. Respiration rates of *O. unicolor* increased between 10 and 20°C, but decreased between 20 and 30°C (Table. 1; Figure 1b; Figure S1).

3.3 | Excretion rates

Mass-corrected *N* excretion rates increased significantly as a response to temperature (Figure 1c; $F_{(2,290)} = 98.468$, $p < 0.001$). Species ($F_{(10,290)} = 26.692$, $p < 0.001$) and the interaction between temperature and species ($F_{[20,290]} = 6.311$, $p < 0.001$) were significant, demonstrating a variable response across our study species. Only *L. ornata* increased across all temperatures, while *E. crassidens*, *F. cerina*, and *O. unicolor* remained constant across all temperatures. For *Amblema plicata*, *O. reflexa*, *Q. rumphiana*, and *T. verrucosa*, N excretion rates only increased between 10 and 20°C, and *C. asperata*, *E. arca*, and *O. unicolor* increased only between 20 and 30°C (Table. 1; Figure 1c; Figure S1).

Mass-corrected P excretion was significantly related to temperature (Figure 1d; Temperature $F_{(2,290)} = 7.857$, $p < 0.001$), but species identity accounted for the greatest variation in rates ($F_{(10,290)} = 12.468$, $p < 0.001$). The species and temperature interaction was also significant ($F_{[20,290]} = 1.864$, $p = 0.016$). Due to the lower effect of temperature, the majority of species had consistent P excretion rates across all temperatures including *C. asperata*, *E. crassidens*, *F. cerina*, *O. reflexa*, *O. unicolor*, *P. decisum*, and *Q. rumphiana*. P excretion increased between 10 and 20°C and decreased between 20 and 30°C for *A. plicata* and *T. verrucosa*. P excretion only increased from 10 to 20°C in *E. arca* and between 10 and 30°C for *L. ornata* (Table 1; Figure 1d; Figure S1). Excretion N:P generally increased with temperature across species (Figure 1f).

3.4 | Thermal sensitivity

Species varied in thermal sensitivity, with seven species classified as thermally tolerant and four demonstrating thermal sensitivity (Table 1; Figure 1e). Anabolism Q_{10} rates exceeded catabolism Q_{10} rates between 20 and 30°C for *A. plicata*, *E. crassidens*, *F. cerina*, *O. reflexa*, *P. decisum*, *Q. rumphiana*, and *T. verrucosa*, indicating that investment in growth and energy storage are likely even at peak summer temperatures. In *C. asperata*, *E. arca*, *L. ornata*, and *O. unicolor*, we saw a decrease anabolism Q_{10} rates compared to catabolism Q_{10} rates, suggesting that these species are breaking down energy stores resulting in declining condition at peak temperatures. These four species span three phylogenetic tribes and two life history strategies suggesting these classifications may not be linked to thermal tolerance.

3.5 | Ecosystem functions

Mussel density at our study site was 20.3 ± 1.8 (mean ± standard error) individuals/m^2 with our tested species making up 90.7% of the community. Across the year, discharge varied dramatically, with most of the high discharge events generally occurring at cool water temperatures and low discharges during warm summer months (Figure 2a). As

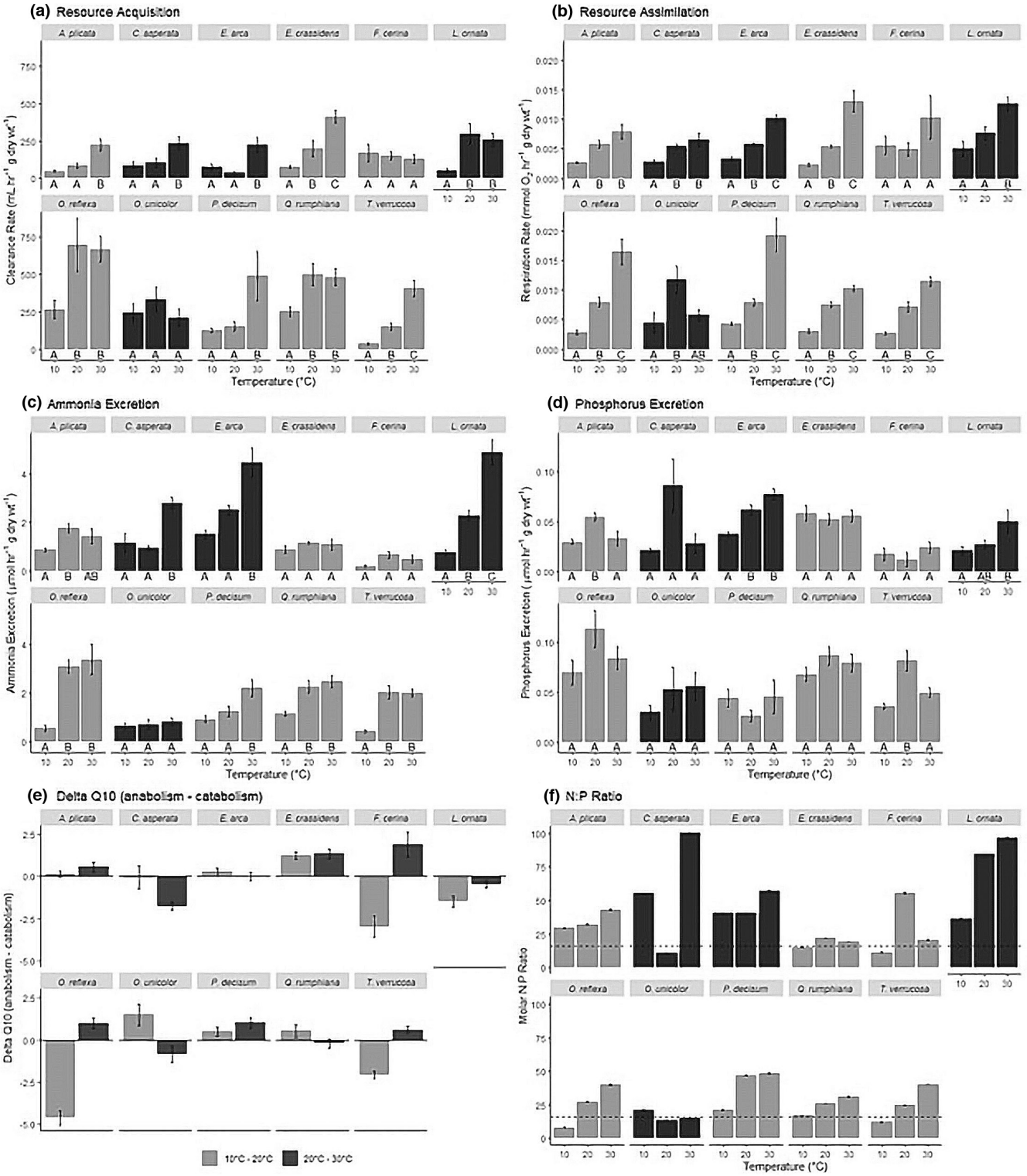

FIGURE 1 Mean (±1 *SE*) (a) clearance rate used to estimate resource acquisition and ecosystem function, (b) oxygen consumption used to estimate resource assimilation and anabolism, (c) ammonia (N) excretion used to estimate catabolism and ecosystem function, (d) phosphorus (P) excretion used to estimate ecosystem, (e) deviation in mean rates (Q10) of anabolism (respiration) and catabolism (ammonia excretion), and (f) molar N:P, dashed line represents the Redfield ratio, as measured for our 11 mussel species across three experimental temperatures (10, 20, 30°C). Light grey bars represent thermally tolerant species, dark grey represents thermally sensitive species. Letters denote significance ($p < 0.05$) determined by a one-way ANOVA followed by a Tukey's post hoc test

a result, mussels contributed more nutrients relative to availability as indicated by volumetric excretion of N and P during summer low flows (Figure 2b,c). The relative importance of our two thermal guilds (i.e., sensitive and tolerant species) to volumetric excretion varied across the year and sensitive species contributions were generally higher particularly at 20°C, but the relative contribution of the two guilds

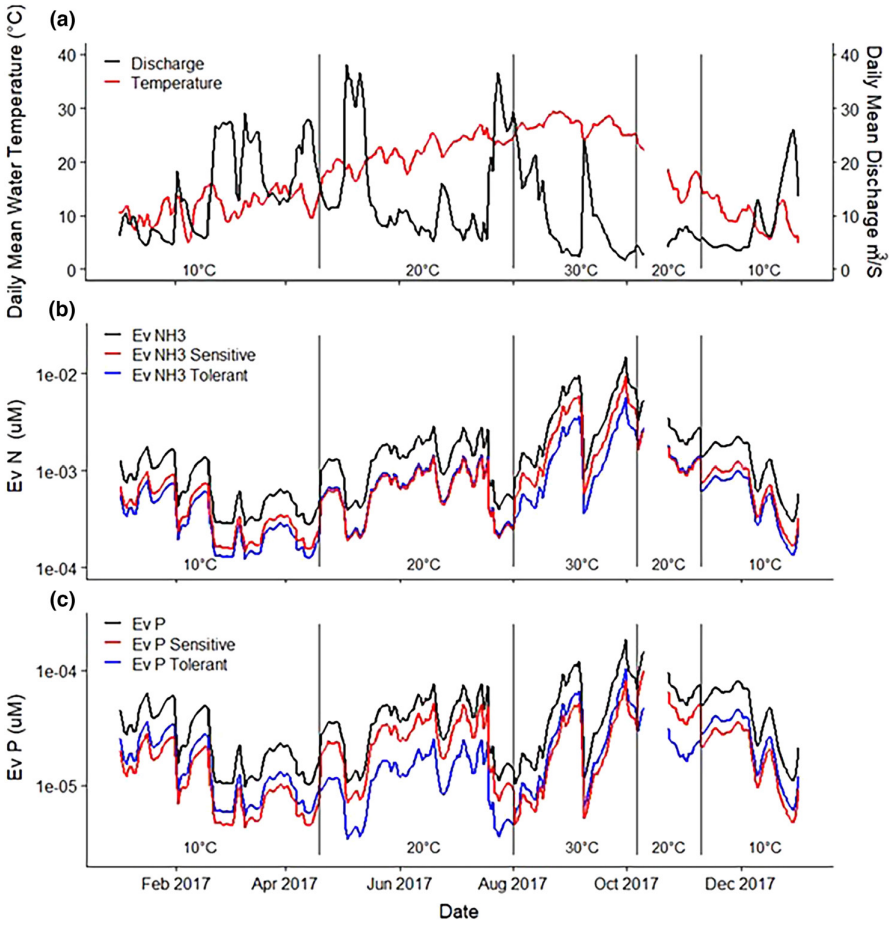

FIGURE 2 (a) Measured temperature and modelled mean daily discharge at our study site on the Sipsey River, Greene County, Alabama. (b) Volumetric excretion of NH_3 modelled throughout the year. (c) Volumetric excretion of phosphorus throughout the year. The black line represents the contribution of the whole community, and the red and blue lines represent the sensitive and tolerant portions, respectively

varied (Figure 2b,c). Sensitive species made up 38.2% of the biomass within the study reach, and tolerant species 61.8% (Figure 3b). At 10 and 20°C, sensitive species contributed less, 31.8% and 33.3% respectively, to community clearance rates, thus they contributed less to filtration than would be predicted by their biomass. However, at 30°C, sensitive species contributed 47.0% of clearance which is greater than predicted by their biomass (Figure 3b). At 30°C, mussels displayed peak community filtration rates coinciding with the lowest flow in the reach. Overall, the mussel community turned over approximately 0.013% and 0.4% of water passing through the experimental reach during high winter flows and lower summertime flows, respectively.

For N and P excretion, sensitive species contributed more than their predicted biomass across all temperatures (N: 54.6%, 47.9%, 61.7%; P: 43.2%, 67.1%, 43.1%; at 10, 20, and 30°C, respectively; Figure 4b). For both N and P excretion rates turnover distance was lowest (N: 108 m; P: 264 m) at 20°C due to the low discharge and background nutrient concentrations and relatively high excretion rates (Table 2; Figure 4c).

4 | DISCUSSION

Climate change is predicted to influence the distribution and subsequent ecosystem functions provided by organisms (Poff et al., 2012; Woodward et al., 2010). Here we show that species-specific thermal regimes influence both the top-down and bottom-up impacts of mussels in riverine ecosystems (Atkinson et al., 2017). Our results highlight that among co-occurring mussel species, distinct physiological responses to temperature modulate the relative impact species have on ecosystem function. The differing physiological response across exposure temperature among mussel species suggests two distinct thermal guilds similar to Spooner and Vaughn (2008), with sensitive species experiencing thermal stress during peak summer temperatures (30°C). We determined co-occurring mussel species had different clearance, respiration, and excretion rates across temperatures as a result of their thermal response. While thermally sensitive species comprised a smaller portion of total mussel community biomass, their nutrient contributions and water clearance rates often comprised the majority of community ecosystem functioning. Annual patterns in abiotic factors (temperature, discharge, and nutrient concentrations) also mediated the relative contribution of mussel communities to pelagic–benthic coupling and the available nutrient pool. While benthic invertebrates are often broadly grouped by taxonomy or trophic guild (e.g., Merritt et al., 2008), this study indicated that species-level physiological traits were different within this single sub-family (Pfeiffer et al., 2019) and functional feeding guild (Huryn & Wallace, 2000). As a result, ecological functions provided by this group vary due to species identity.

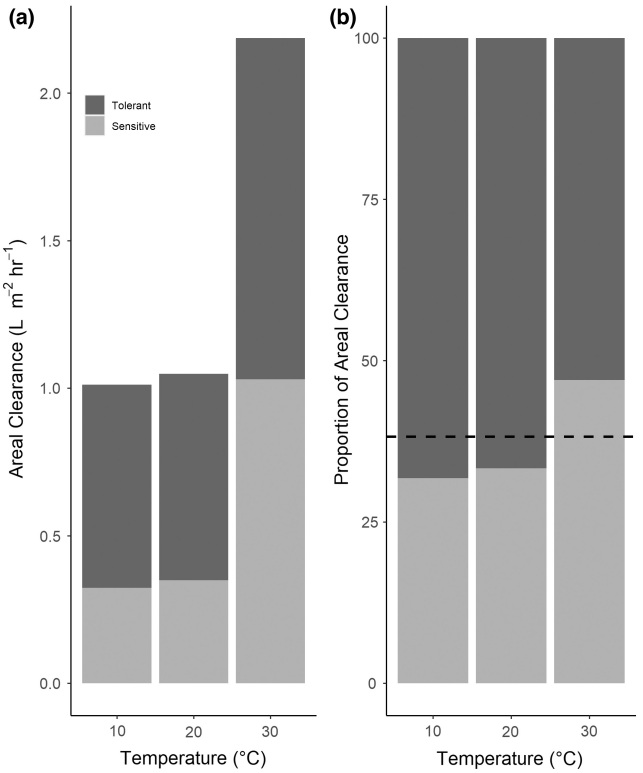

FIGURE 3 (a) Areal clearance rate for the study mussel bed and (b) the proportion of areal clearance rate provided by the tolerant and sensitive species in the community as classified in Table 1. The dotted line represents the proportion of biomass of the tolerant and sensitive species at our study site

4.1 | Physiological rates vary across species and temperature

Freshwater mussels, as any other ectotherm, are expected to have greater physiological demands with increasing temperatures (Gillooly et al., 2001). Generally, this was the case for clearance, respiration, and N excretion rates across the mussel species studied here. Temperature explained the greatest variation in physiological rates and most species had their peak rate at 30°C. However, for many of the species evaluated there was not a significant difference in many of the physiological rates between 20 and 30°C and Q_{10} values were higher for 10–20° than 20–30°C. Work on other aquatic species has also highlighted that physiological rates increase with temperature often initiating a severe stress responses or resource limitation that can directly or indirectly diminish growth rates (Spooner & Vaughn, 2008; Pennock et al. 2021).

While temperature explained most species-specific variation among clearance, respiration, N excretion, and P excretion rates, a significant portion of variation was explained by species. Differences in rates across species can be partially explained by differences in body size as rates scaled similarly to 0.75 as predicted by Metabolic Theory of Ecology (Brown et al., 2004). While temperature was a significant factor predicting P excretion, species identity explained most the variation. Although nutrient uptake rates and nutrient limitation status in our system is unknown, P is often a limiting nutrient in freshwater ecosystems so it may be more highly conserved by animals than N in meeting metabolic demand (Hecky & Kilham, 1988). Patterns in P excretion rates may also be driven by species-specific stoichiometric tissue requirements, or demand for P-rich rRNA needed to support fast growth (Atkinson, van Ee, & Pfeiffer, 2020; Elser et al., 2000). Previous work in this system has shown that faster growing species have higher soft tissue P (Atkinson, van Ee, & Pfeiffer, 2020), thus they have greater P demand to maintain homeostasis. Interestingly, two of these faster growing species, *L. ornata* and *O. unicolor*, were categorised as thermally sensitive, suggesting greater P demand under periods of enhanced thermal stress.

4.2 | Thermal tolerance varies across species

Of 11 species evaluated, *C. asperata*, *E. arca*, *L. ornata*, and *O. unicolor* had a shift towards catabolism at 30°C, suggesting that they were experiencing thermal stress as energy usage exceeded resource assimilation. This thermal stress could result in mortality in the case of prolonged exposure to peak temperatures. Remaining species responses indicated thermal tolerance with resource assimilation meeting metabolic demands that would result in continued investment in growth at peak summer temperature. Previous studies found *A. plicata*, *O. reflexa*, and *F. flava* (sister species of *F. cerina*) to be thermally tolerant, and *Lampsilis cardium* (sister species of *L. ornata*) and *Cyclonaias pustulosa* (sister species of *C. asperata*) to be thermally sensitive (Baker & Hornbach, 2001; Ganser et al., 2013; Spooner & Vaughn, 2008), which is congruent with our findings. Thermal preferences were not associated with a particular mussel life history strategy, suggesting that these thermal preferences are not related to the widely adopted life strategy classification (Haag, 2012). However, three of the four sensitive species were classified as periodic or periodic/opportunistic, suggesting that shorter-lived species may be less resistant to warm temperatures. A first look at these data also suggests some phylogenetic constraints in response to thermal tolerance, as, generally, many of the Lampsilini (e.g., *Actinonaias ligamentina*, *L. cardium*, *L. ornata*, *O. unicolor*) appear to be among the most sensitive. However, *Obliquaria reflexa*, another Lampsilini, demonstrated thermal tolerance in this study and also in Oklahoma (Spooner & Vaughn, 2008). More work across a broader group of species and localities and across seasons that vary in temperature will be useful for understanding how thermal optima are distributed across life history strategies across the Unionidae phylogeny.

4.3 | Mussel community contributions to ecosystem function vary temporally

Sensitive species supported a disproportionate portion of community water clearance at 30°C. This is probably due to the metabolic

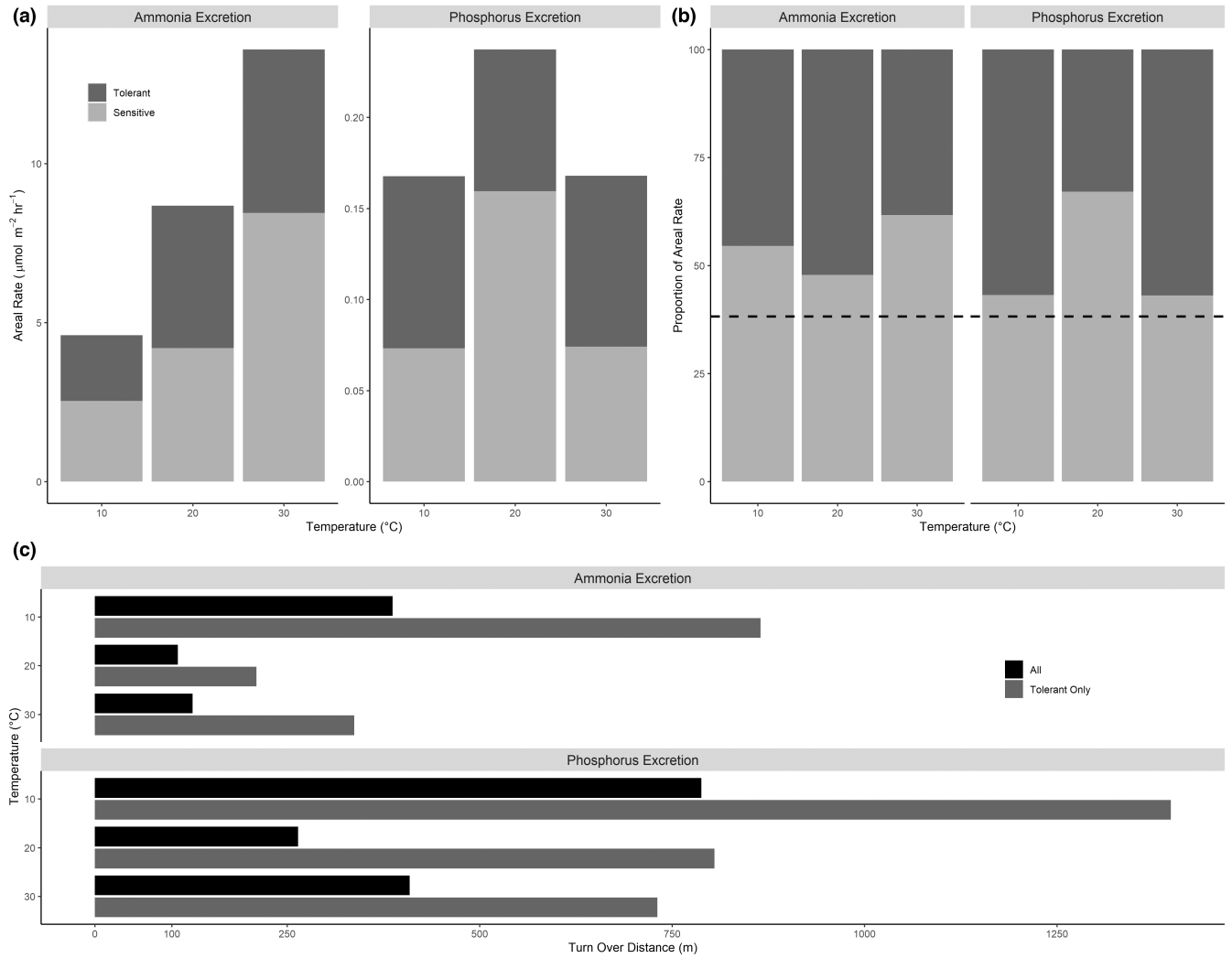

FIGURE 4 (a) Areal rates for our study mussel bed for ammonia (N) and phosphorus (P) excretion. (b) Proportion of areal rates contributed by our two thermal guilds. The dotted line represents the proportion of biomass of tolerant and sensitive species in the community. Sensitive species contribute a greater proportion of the ecosystem function than their biomass would predict. (c) Modelled turnover distance for water moving through a continuous mussel bed the density of the study mussel bed, showing how long it would take for the community to completely turn over N and P

TABLE 2 Mean daily discharge, ammonia (N), and phosphorus (P) concentrations in the study reach at experimental temperatures (±2°C)

	Daily Reach discharge			Ammonia (N)			Phosphorus (P)		
Temperature (°C)	Mean (m^3/s)	*SD*	*n* (days)	Mean (µmol/L)	*SD*	*n*	Mean (µmol/L)	*SD*	*n*
10	12.7	5.98	52	0.470	0.095	9	0.0348	0.0065	9
20	7.10	5.44	75	0.441	0.143	12	0.0294	0.0079	12
30	5.50	1.28	61	1.048	0.337	9	0.0415	0.0092	9

stress thermally sensitive species are experiencing, resulting in higher clearance rates as a means to meet heightened metabolic demands. Compared with Spooner and Vaughn (2008), our mass-corrected clearance rates are higher, but clearance times of our community was lower, which may be explained in part by differences in mussel body size and stream discharge between study rivers (Vaughn et al., 2004). However, it is important to note that the measured rates may vary seasonally due to longer term acclimatisation to thermal conditions (Hornbach et al., 1983). Thus, future studies should also assess variation in these temperature-dependent rates across time.

For both N and P excretion, mussels contributed more at low flows and warmer temperatures similar to previous findings

(Spooner & Vaughn, 2008). Sensitive species contributed more to nutrient demand across all temperatures than their biomass would predict in comparison to the tolerant species. It is not clear why sensitive species are excreting more across all temperatures, but differences in tissue N:P ratios among species and the N:P of the resources pools they are acquiring seem to contribute (Atkinson, van Ee, & Pfeiffer, 2020). Temperature treatments increased N excretion more than P excretion resulting in differences in N:P ratio across temperature. At low temperatures, many species were excreting near or below the Redfield ratio (16:1, N:P) (Redfield, 1958), which may favour periphyton and heterotrophic bacteria that are P limited (Hall et al., 2005). As temperature increased, the excretion N:P ratio increased, which may favour microbial communities that have a higher N demand at warmer temperatures. This increase in N provisioning by sensitive species also altered the overall stoichiometric ratio of their excretion compared to tolerant species, which maintain a lower N:P ratio at peak temperature.

Nutrient turnover distance varied as a function of both stream discharge and temperature, similar to what has been found in previous studies of other aquatic organisms (Benstead et al., 2010; McIntyre et al., 2008). During periods of high flow, the contribution of mussel derived ecosystem functioning as estimated by volumetric excretion and turnover, was decreased by an order of magnitude; even when temperature and excretion rates were high. The distance it took for the mussel community to turnover the N and P pools present in the river was low across all temperatures, but was greatest at 20°C due to relatively low discharge and lower background concentrations of N and P in the river. However, despite the strong, seasonal bottom-up effects mussels have, mussels co-occur with fish, and recent work suggests that grazing mobile fish leads to a more consistent and homogeneous supply of resources (Vaughn et al., 2022), thus their combined influence on ecosystem function is likely to be important. In addition, our excretion rates were lower in these lab trials than in field trials on the same species (Hopper et al., 2021) and in comparison to previous field measurements on similar species (Atkinson & Vaughn, 2015), suggesting that laboratory rates may underestimate mussel contributions in-situ. Lower rates may be attributable to differences in food resources between lab trials and natural settings. Future work measuring both clearance and excretion rates should strive to mimic field conditions to capture more realistic physiological rates that can be extrapolated to the field.

4.4 | Conclusions and future implications

Physiological rates relevant to ecosystem functioning of mussels are highly temperature dependent, although species and life stages respond differently across temperatures and seasonally (Christian et al., 2008; Hornbach et al., 1983; Pandolfo et al., 2010; Spooner & Vaughn, 2008). Species-specific traits modulate ecosystem functioning, especially temporally with annual temperature regime. Abiotic factors also mediated ecosystem function supported by mussels, with high flows in winter, and higher nutrient concentrations in summer, lowering the relative contribution of the community. As a result, thermally sensitive species support higher clearance rates and nutrient provisioning during summer temperatures, driven by high metabolic demand.

Freshwater mussels are already experiencing dramatic declines throughout their range primarily due to anthropogenic alterations to freshwater habitats and extended drought, specifically when flows cease, which can result in high mussel mortality (Garrido Nogueira et al., 2021; Golladay et al., 2004; Paschoal et al., 2020; Strayer et al., 2004; Vaughn & Hoellein, 2018). Further changes to freshwater ecosystems due to changes in climate and human demand for freshwater are likely to exacerbate this decline. High temperatures due to droughts can be detrimental to thermally sensitive species, and low temperatures from bottom-release dams can disrupt other aspects of mussel biology (Atkinson et al., 2014; Galbraith & Vaughn, 2011). As mussel species are lost, specific species traits will be removed from the community, with lost biomass unlikely to be replaced by more tolerant species given their long-life span (Dubose et al., 2019; Vaughn et al., 2015). In the face of rapid climate change, freshwater animal distributions could shift to more favourable habitats (Poff et al., 2012). However, the fragmented nature of river habitats (e.g., dams, increased length and duration of dry reaches) is a particular challenge to dispersal by mussels as they are dependent on mobile fish hosts (Garrido Nogueira et al., 2021; Lopes-Lima et al., 2018; Paschoal et al., 2020). As we look for management solutions that reduce stress and mussel species extirpation, we need a better understanding of how mussels respond to temperature challenges within currently occupied habitats and how this might favour species with particular life history strategies and phylogenetic constraints. With so few data available regarding thermal preferences and ecosystem functions provided by most freshwater mussel species, future work should strive to fill these data gaps for this imperilled group.

AUTHOR CONTRIBUTION

Conceptualisation: B.C.V., P.D.J., C.L.A. Developing methods: B.C.V., C.L.A. Conducting the research: B.C.V., C.L.A. Data analysis: B.C.V. Preparation of figures and tables: B.C.V., C.L.A. Data interpretation and writing: B.C.V., P.D.J., C.L.A.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data that supports the findings of this study including the raw filtration, excretion, and respiration data are published on FigShare 10.6084/m9.figshare.16918093.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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