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A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling

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Abstract The sustained decline in habitat quality and community integrity highlights the importance of understanding how communities and environmental variation interactively contribute to ecosystem services. We performed a laboratory experiment manipulating effects of acclimation temperature (5, 15, 25, and 35°C) on resource acquisition, assimilation and subsequent ecosystem services provided by eight freshwater mussel species. Our results suggest that although freshwater mussels are broadly categorized as filter feeders, there are distinct nested functional guilds (thermally tolerant and sensitive) associated with their thermal performance. At 35°C, thermally tolerant species have increased resource assimilation and higher rates of contributed ecosystem services (nutrient excretion, benthic–pelagic coupling). Conversely, thermally sensitive species have decreased assimilation rates and display an array of functional responses including increased/decreased benthic–pelagic coupling and nutrient excretion. Although thermally sensitive species may be in poorer physiological condition at warmer temperatures, their physiological responses can have positive effects on ecosystem services. We extrapolated these results to real mussel beds varying in species composition to address how shifts in community composition coupled with climate change may shift their contributed ecological services. Comparative field data indicate that two co-existing, abundant species with opposing thermal performance (*Actinonaias ligamentina*, *Amblema plicata*) differentially dominate community biomass. Additionally, communities varying in the relative proportion of these species differentially influence the magnitude (benthic–pelagic coupling) and quality (N:P excretion) of ecosystem services. As species are increasingly threatened by climate change, greater emphasis should be placed on understanding the contribution of physiological stress to the integrity and functioning of ecosystems.

Keywords Unionidae · Ecosystem service · Community · Nutrient excretion · Biodiversity

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Introduction

The sustained decline in habitat quality and community integrity highlights the importance of understanding the interactive contribution of communities and environmental variation to ecosystem services (Bond and Chase 2002; Cardinale et al. 2005). Most studies addressing this issue identify parameters that promote or limit patterns of species distributions and diversity, including biogeography, physiological tolerances, and resource requirements (Petchey et al. 2002), such that species in a community exist as a net result of overcoming various stressors to acquire, assimilate, and convert resources into biomass and offspring (Tilman 1986). Recently, studies have examined

the functional significance of community structure by asking how species interactions influence services such as productivity, invasibility and stability (Naeem et al. 1994; Wardle and Peltzer 2003). These studies assume that competitive and facilitative interactions occur between species, and that their functional traits enhance or inhibit ecosystem services (Loreau and Hector 2001).

Performance-based species traits vary along ecological gradients (Cottenie 2005), thus the degree to which species' traits match the environment should dictate both where species can live and how they contribute services to the ecosystem (Ackerly 2003). Positive species richness effects on productivity have been perceived to result from increased species performance, and species in good condition contribute a greater magnitude of services (Fridley 2001; Hooper 1998). However, communities include species with distinct functional traits that perform differently under variable environmental conditions (Petchey and Gaston 2002). Additionally, it is also important to understand how community structure influences the functional contributions of species in sub-optimal environments (Petchey et al. 2002). Climate change threatens to offset the synchrony of species' traits and the environmental landscape by pushing organisms beyond their biologically stable limits. These shifts influence not only species distributions, and ultimately local and regional species pools, but also the services they provide to ecosystems. Thus, there is a need to understand how species' performances change along environmental gradients. This is particularly important in aquatic systems, where shifts in habitat quality associated with environmental perturbations threaten the integrity of fish (Morgan et al. 2001) and macroinvertebrate (Strayer et al. 2004) communities. This study examines how species' traits influence ecosystem services under different thermal regimes and with varying community composition, using freshwater mussels as a model system.

Freshwater mussels (Bivalvia: Unionidae) are a guild of filter-feeding, sessile, burrowing bivalves that occur in speciose aggregations (mussel beds) that dominate the benthic biomass of many eastern North American lakes and streams (Strayer et al. 1981). Because of their large biomass and filtering abilities, they link benthic and pelagic compartments by removing particulate matter from the water column and transferring it to the sediment, in turn subsidizing benthic algae and invertebrates via nutrient mineralization and organic matter biodeposition (Christian et al. 2004; Spooner and Vaughn 2006). Freshwater mussel communities are currently in an unprecedented state of decline with over 70% of known North American species (>296 described) listed as threatened, endangered, or of special concern (Williams et al. 1993). Because mussels are thermo-conformers with limited mobility, they are particularly sensitive to alterations in flow and temperature. In the southern United States, both natural and human-induced low-flow periods usually occur during the summer and can result in fragmentation of rivers into isolated pools. Stream temperatures track air temperatures (Covich et al. 1997) because of high rates of evapotranspiration (Mulholland et al. 1997). Summer water temperatures often average 35°C and can exceed 40°C, which is at or above the thermal limit of many mussel species. The magnitude of ecological services performed by mussels is greatest under these extreme physical conditions (Spooner and Vaughn 2006; Vaughn et al. 2007) and is likely related to increase metabolic costs at these high temperatures (Portner 2002). Rivers in this area are considered particularly vulnerable to climate warming (Matthews et al. 2005), as mussel populations and their fish hosts cannot migrate northward because of prevailing west-to-east major drainages (Covich et al. 1997; Matthews and Zimmerman 1990).

To determine how differences in functional traits between freshwater mussel species contribute to differences in ecosystem function under diverse thermal regimes we quantified various measures of resource acquisition, resource assimilation, and resulting ecosystem services for a natural assemblage of mussels. We then extrapolated our results to actual mussel beds from the southern United States that vary in species composition to address how shifts in community composition coupled with changes in thermal regimes that may occur with climate change will influence ecological function in these rivers.

Materials and methods

We measured rates of resource acquisition, resource assimilation, and ecosystem services for eight mussel species at four different temperatures. Mussels were collected from the Little River in southeastern Oklahoma, United States. Over 35 mussel species are known from this river, but most are relatively rare (Vaughn and Taylor 1999). We chose species that: (1) were common and thus could be important to river ecosystem processes; and (2) encompassed the natural range of sizes, life histories and phylogenetic histories, and thus represent the range of mussel functional traits in the river. Additionally, these species are widely distributed throughout the Mississippi River drainage basin, and thus, represent communities that we expect to be highly impacted by climate change (anomalous temperature and drought events). We collected 40 individuals each of *Actinonaias ligamentina* (Lamarck, 1819) (244.9 mm mean shell length ± 9.2), *Amblema plicata* (Say, 1817) (202.5 ± 9.9), *Megalonaias nervosa* (Rafinesque, 1820) (406.2 ± 30.8), *Lampsilis cardium* (Rafinesque, 1820) (139.7 ± 8.4), *Fusconaia flava* (Rafinesque, 1820) (75.8 ± 4.4), *Truncilla truncata*

(Rafinesque, 1820) (43.3 ± 1.9), *Obliquaria reflexa* (Rafinesque, 1820) (45.4 ± 2.5), and *Quadrula pustulosa* (Lea, 1831) (57.2 ± 3.9). Biofilm was gently removed from mussel shells (Spooner and Vaughn 2006), and mussels were maintained in the laboratory at typical river temperature (15°C) prior to the experiment.

Although we initially suspected that differences may present themselves at warmer temperatures, we had no a priori directional prediction and therefore chose treatments (5, 15, 25, and 35°C) that represent the natural range and extremes of temperatures experienced by mussels in the south-central United States. Mussels were acclimated to experimental temperatures over a period of 2 weeks in separate 500-l Frigid Units re-circulating streams. For the duration of acclimation, mussels were fed a mixed assemblage of cultured algae (green algae and diatoms) seeded from water collected in the Little River. Prior to each experimental run, mussels were held without food in separate holding tanks for 24 h to clear their guts. Experiments were performed on individual mussels in four, 1.8-m^3 environmental chambers which allowed precise control of water temperature. On each day over a period of 20 days, each chamber was randomly assigned a temperature, four randomly selected mussels individuals (without replacement), and a non-mussel control (water only) to account for confounding water chemistry associated with microbial activity. Over the course of the experiment, measurements were performed on ten individuals of each species and controls for each temperature.

For each mussel and control, the following was performed: individuals were placed in a glass beaker (500 ml for small mussels, 1,500 ml for large mussels) with a stir bar, fed an initial aliquot of cultured algae (89.7 mg C l^{-1}), a 50-ml water sample was collected for chlorophyll *a* analysis, and beakers were placed on stir plates in the environmental chambers. Mussels were allowed to filter feed for 1.5 h, after which beakers were removed from the chambers and feces and pseudofeces (particles rejected during feeding) collected with a pipette and filtered (glass fiber filter GF/F). We recorded water volume, then filtered the water (glass fiber filter GF/F) and froze the filter. Each mussel was gently washed and placed in a covered glass respirometer (500 ml for small mussels, 1,500 ml for large mussels) with a stir bar and filtered water. We collected water samples from each respirometer for nutrient analysis and measured O_2 concentration with an Orion O_2 meter. Respirometers were placed in environmental chambers, stirred for 1.5 h, then were removed, O_2 was measured, two additional 10-ml water samples were collected, and water volume was recorded. We recorded the shell length and wet weight of each mussel and took a 20- to 40-mg mantle tissue sample for glycogen analysis (Berg et al. 1995). We then dried mussels and determined dry weight (tissue + shell).

Resource acquisition

We used mass-specific clearance rates (the volume of water from which a mussel has filtered all algal particles) as our measure of resource acquisition using the following equation (Horgan and Mills 1997).

$$CR = V \ln(conc_i/conc_f)(M\,t)^{-1}$$

CR is clearance rate (volume of water filtered g^{-1} dry weight h^{-1}), V is water volume (l), $conc_i$ is initial algal concentration (mg chl *a* l^{-1}), $conc_f$ is final algal concentration (mg chl *a* l^{-1}), M is dry mass (g), and t is time (h). Chlorophyll *a* was extracted and quantified from frozen glass fiber filters using the acetone method (APHA 1996).

Resource assimilation

We used respiration rates (Q_{10}) and tissue glycogen concentration as measures of resource assimilation. Mass-specific O_2 consumption was calculated as the change in O_2 concentration over time corrected for respirometer volume and mussel dry mass. Our final O_2 concentrations were above 50% saturation for most trials, and we assumed that O_2 consumption rates were linear. All respiration measurements were corrected for O_2 changes associated with control treatments.

We compared the rates of net catabolic processes to anabolic processes to determine the overall condition of mussels relative to their thermal treatment. We used Q_{10} values of O_2 consumption as a surrogate index of rates of anabolism, and Q_{10} values of NH_3 excretion as a surrogate index of rates of catabolism. Q_{10} values quantify the relative change in reaction rate between two temperatures differing by 10°C. Since different individuals were used for each treatment, it was not possible to calculate Q_{10} values on the same individuals, therefore, mean O_2 and NH_3 excretion values for each treatment for each species were used to calculate Q_{10} rates. Net Q_{10} rates were calculated as the deviation in assimilation and catabolism rates. Mantle tissue glycogen concentration was quantified using the phenol-sulfate method (Naimo et al. 1998).

Ecosystem services

We used NH_3, P, molar N:P excretion and biodeposition rates as measures of ecosystem services. Nutrient samples were analyzed spectrophotometrically according to standard methods using the phenate method for NH_3, and the ascorbic acid method with persulfate digestion for P (APHA 1996). Molar N:P was calculated as the ratio of NH_3 (assuming minimal urea production) to P excreted. Biodeposition rates were determined as the ash-free dry

weight of feces and pseudofeces (APHA 1996). All mass-specific excretion and biodeposition rates were corrected for background nutrients or organic matter evolved in control treatments over the duration of the experiment.

Extrapolation of results to natural mussel beds

We extrapolated our data to nine mussel beds in three rivers (Kiamichi River, Little River and Ouachita River) in the Ouachita Uplands biogeographic province of south-eastern Oklahoma and western Arkansas. We chose these rivers because they are relatively undisturbed, are very well known to us through previous work and contain diverse, healthy mussel assemblages (Vaughn and Spooner 2006). For each bed, we measured mussel densities in 15 randomly placed 0.25-m^2 excavated quadrats (Vaughn et al. 1997). We recorded the shell length of all sampled individuals and returned them alive to the mussel bed. We determined the areal extent of mussel beds and multiplied this by mussel density to estimate the number of mussels in each bed. Species-specific length-dry weight regressions were used to estimate mussel biomass.

In general, most communities are log-normally distributed with a few abundant species followed by many rarer species. In our case, our eight experimental species always represented the most common species in the community. These species accounted for over 96% of the total mussel biomass in seven of the beds and 85–76% respectively in the remaining two. The residual biomass of these beds (<4, 15, and 24%) is broadly distributed among a handful of individuals representing up to eight additional species. Since we were interested in the effect of species with known traits under different environmental conditions, we assumed the impacts of non-experimental species were negligible and excluded them from the model. We recognize, however, the possibility that these excluded species could have disproportionate effects on ecosystem services, but given their low relative biomass, we believe this is unlikely.

Mussel bed excretion estimates were calculated by multiplying species-specific excretion rates (mg P l^{-1} h^{-1} g^{-1} dry weight, mg NH_3 l^{-1} h^{-1} g^{-1} dry weight) by their respective site biomass (g dry weight). P and N contributions were then summed for each species and converted to molar N:P ratios. Water column turnover rates were estimated by multiplying water clearance rates (l h^{-1} g^{-1} dry weight) for each species by their respective site biomass (g dry weight) over the duration of 24 h. Daily clearance rates were then summed for each species and divided by the total volume of water passing over the mussel bed over the duration of 24 h. We estimated water volume by multiplying stream flow by the areal extent of the mussel bed. We conservatively estimated stream flow to be 0.05 m s^{-1} which is well within the range of flows experienced by mussels in the summer (0.01–0.43 m s^{-1}; D. E. Spooner, unpublished data). We present the clearance extrapolation as the number of times the water column has been processed by the mussel bed over the duration of 24 h.

Data analyses

We used ANOVA with Sidak post hoc procedures to compare effects of independent variables—species, temperature, and species × temperature on dependent variables—acquisition (clearance rate), assimilation (O_2 consumption and glycogen concentration), and ecosystem services (biodeposition rate, NH_3 and P excretion rates). Dependent variables were log transformed to meet assumptions of variance homogeneity. We used linear regression to determine the relative influence of species composition on mussel bed nutrient dynamics and water column turnover. All statistical analyses were performed using SPSS software (SPSS 2006).

Results

Resource acquisition

Mass-specific clearance rates increased with temperature (Fig. 1a). Highest rates were at 35°C for all species except *A. ligamentina*, *L. cardium* and *T. truncata*, which had greatest clearance rates at 25°C and declined at 35°C [Fig. 1a; Temperature, $F_{(3,268)} = 75.936$, $P < 0.001$; Species × Temperature, $F_{(21,268)} = 4.151$, $P < 0.001$]. Differences between species were largely due to higher mass-specific clearance rates in smaller-bodied mussel species [Species, $F_{(7,268)} = 9.219$, $P < 0.001$].

Resource assimilation

Mass-specific O_2 consumption rates increased with temperature and were highest at 35°C for all species except *A. ligamentina*, *L. cardium*, and *T. truncata*. These species had highest mass-specific O_2 consumption at 25°C and declined at 35°C, suggesting that thermal stress may cause these species to become partially anaerobic [Fig. 1b; Species, $F_{(7,268)} = 17.171$, $P < 0.001$; Temperature, $F_{(3,268)} = 51.909$, $P < 0.001$; Species × Temperature, $F_{(21,268)} = 3.781$, $P < 0.001$].

Anabolism rates (Q_{10} O_2) exceeded catabolism rates (Q_{10} NH_3) for *A. plicata*, *F. flava*, *M. nervosa*, and *O. reflexa*, indicating that investment into growth or maintenance may still be occurring at 35°C (Fig. 2). However, rates of anabolism were considerably lower than catabolism rates for

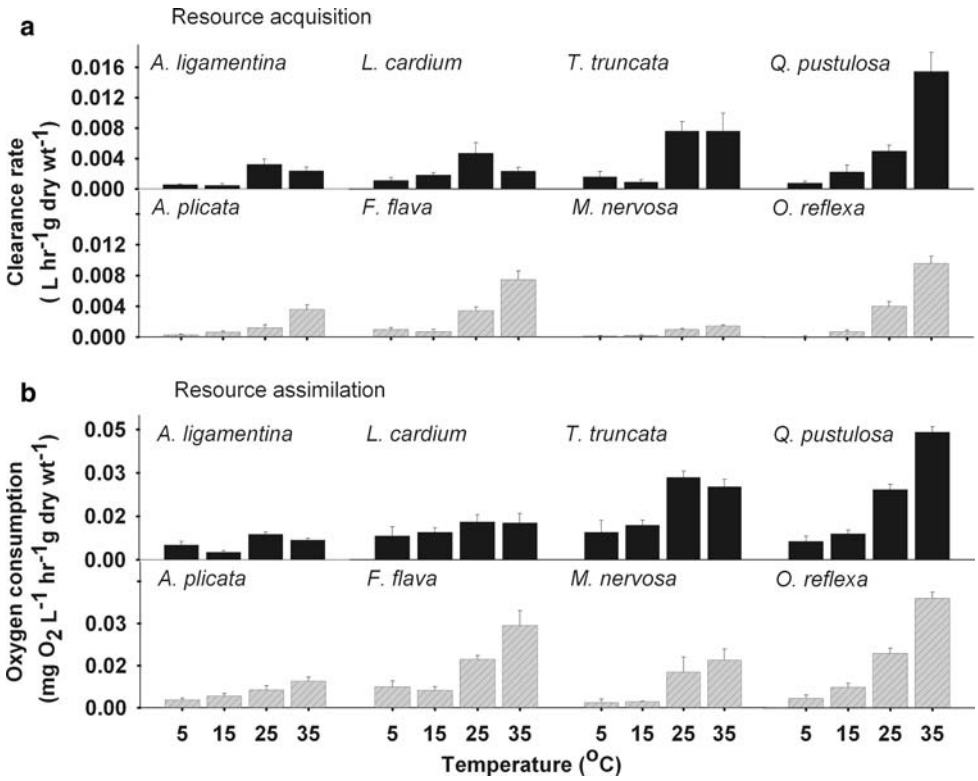

Fig. 1 Mean (+1 SD) **a** resource acquisition measured as clearance rate and **b** resource assimilation measured as O_2 consumption for eight mussel species at four experimental temperatures (5, 15, 25, 35°C). *Filled bars* represent thermally sensitive species (*Actinonaias ligamentina*, *Lampsilis cardium*, *Quadrula pustulosa*, *Truncilla truncata*) and *hatched bars* represent thermally tolerant species (*Amblema plicata*, *Fusconaia flava*, *Megalonaias nervosa*, *Obliquaria reflexa*)

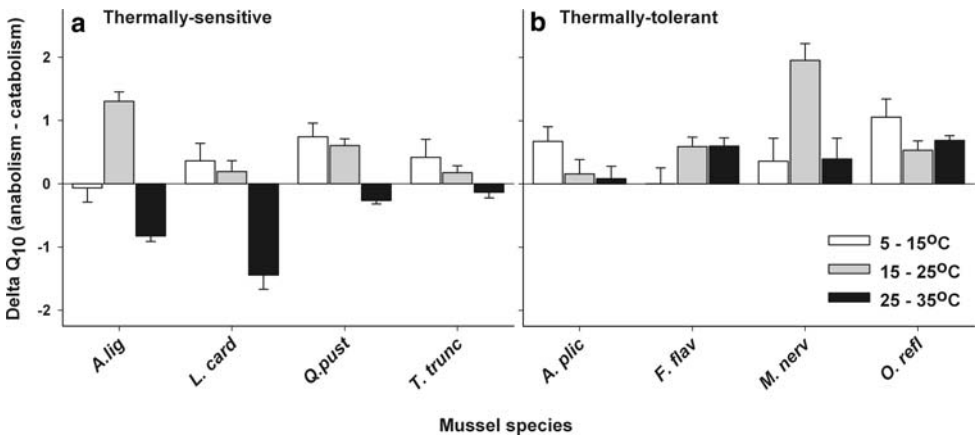

Fig. 2 Deviation in mean (+1 SD rates (Q_{10}) of anabolism and catabolism for **a** thermally sensitive and **b** thermally tolerant mussel species. *White bars* represent differences in rates between 5 and 15°C, *gray bars* differences in rates between 15 and 25°C, and *black bars* differences in rates between 25 and 35°C

A. ligamentina, *L. cardium*, *T. truncata*, and *Q. pustulosa*, indicating that protein breakdown and/or glycogen catabolism may be occurring, resulting in a decline in condition (Fig. 2).

Mantle glycogen concentrations were highly variable and differed significantly between species [$F_{(7,274)} = 9.711$, $P < 0.001$]. Temperature alone did not have a significant influence on glycogen concentration [$F_{(3,274)} = 0.777$, $P > 0.05$]. This may indicate that a longer time period or higher magnitude of stress is required before glycogen is mobilized. However, there was a significant interaction between temperature and species with both *A. ligamentina* and *L. cardium*, with lowest glycogen concentrations at 35°C [$F_{(15,274)} = 2.486$, $P = 0.003$; Electronic supplementary material 1 (ESM1)], which indicates that these two species may use carbohydrate catabolism as an energetic supplement.

Ecosystem services

NH_3 production increased steadily with temperature for all species and was highest at 35°C, with the exception of *T. truncata* and *M. nervosa*, for which it tapered off [Fig. 3; Species, $F_{(7,268)} = 5.949$, $P < 0.001$; Temperature, $F_{(3,268)} = 61.432$, $P < 0.001$; Species × Temperature, $F_{(21,268)} = 2.021$, $P = 0.006$; ESM1]. Despite having

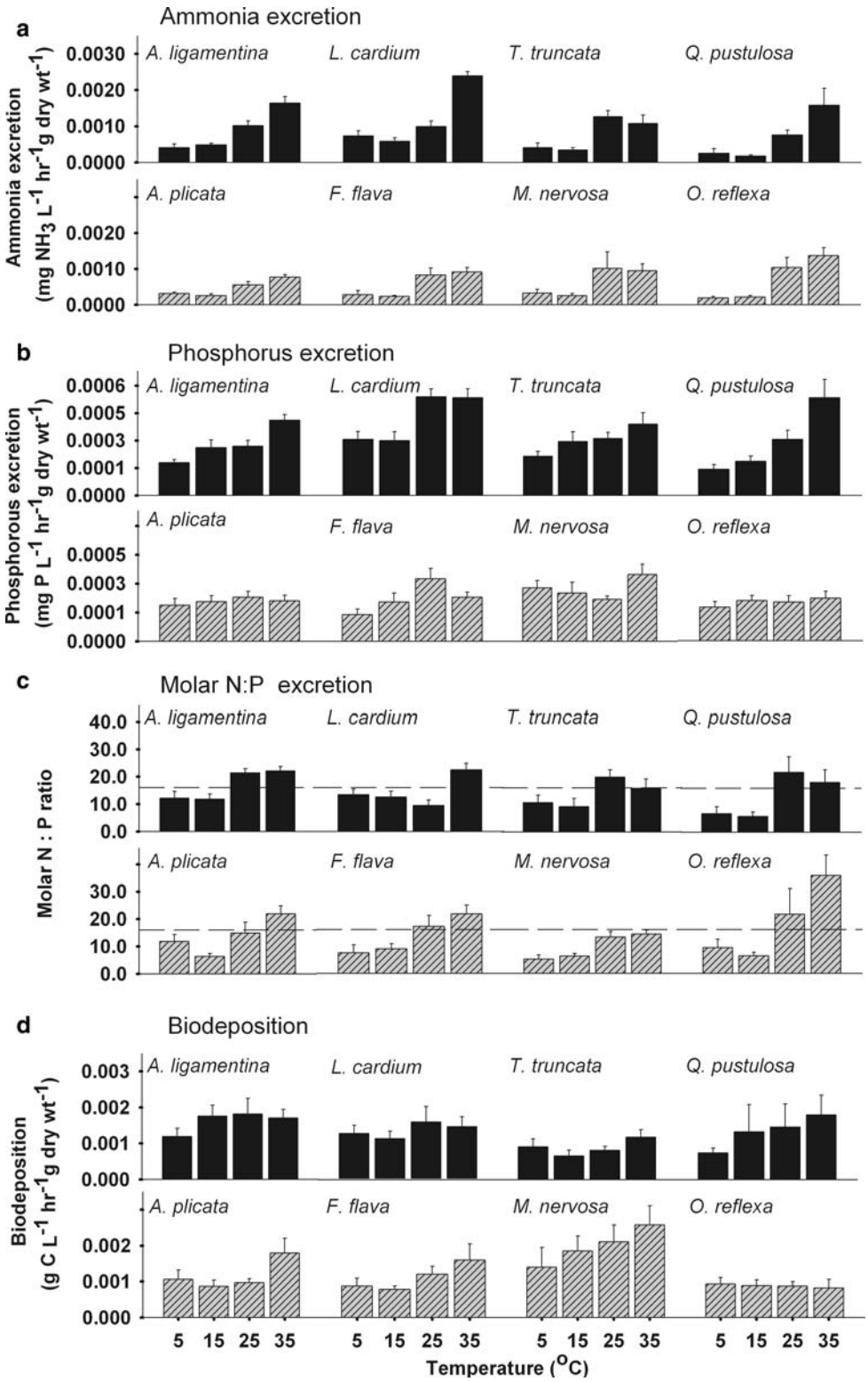

Fig. 3 Effect of acclimation temperature on mean (+1 SD) **a** NH_3 excretion rate, **b** P excretion rate, **c** molar N:P excretion rate (*hashed line* represents Redfield ratio), and **d** biodeposition rate for eight mussel species across the four experimental temperatures. *Filled bars* represent thermally sensitive species and *hatched bars* represent thermally tolerant species

larger body sizes, *A. ligamentina* and *L. cardium*, along with *Q. pustulosa* had highest mass-specific NH_3 excretion rates at 35°C relative to other species (Fig. 3). P excretion also increased with temperature, with highest rates at 35°C for *A. ligamentina*, *L. cardium*, *T. truncata*, and *M. nervosa* [Fig. 3; Species, $F_{(7,268)} = 3.533$, $P = 0.007$; Temperature, $F_{(3,268)} = 4.111$, $P < 0.001$; Species × Temperature, $F_{(21,268)} = 1.073$, $P > 0.05$). *F. flava* had highest excretion rates at 25°C, while *A. plicata* and *O. reflexa* had negligible differences in excretion rates (ESM1).

Temperature and species-specific excretion rates led to considerable variability in N:P excretion rates [Fig. 3; Species: $F_{(7,268)} = 6.166$, $P < 0.001$; Temperature: $F_{(3,268)} = 20.754$, $P < 0.001$; Species × Temperature: $F_{(21,268)} = 1.476$, $P = 0.006$). At cooler temperatures (5–15°C), molar N:P ratios were similar for all species varying from 6 to 16. At 25°C, N:P excretion rates increased with the exception of *L. cardium* which decreased (Fig. 3; ESM1). Biodeposition rates were also highly variable and differed between species [$F_{(7,268)} = 11.662$, $P < 0.001$] and temperature [$F_{(3,268)} = 8.700$, $P < 0.001$] without any significant interaction between the two [$F_{(21,268)} = 0.000$, $P > 0.05$; Fig. 3].

Extrapolation

N:P excretion rates for whole mussel beds increased as a function of the biomass of one species, *A. ligamentina*, in the mussel bed at 15°C [$F_{(1,8)} = 7.294$, $R^2 = 0.510$, $P = 0.031$], 25°C [$F_{(1,8)} = 7.369$, $R^2 = 0.513$, $P = 0.030$], and 35°C [$F_{(1,8)} = 5.315$, $R^2 = 0.432$, $P = 0.055$; Fig. 4]. Relative biomass of *A. plicata* had no significant effect on overall N:P excretion at 15°C [$F_{(1,8)} = 3.711$, $R^2 = 0.346$, $P = 0.095$], 25°C [$F_{(1,8)} = 3.840$, $R^2 = 0.354$, $P = 0.091$], or 35°C [$F_{(1,8)} = 3.442$, $R^2 = 0.330$, $P = 0.106$]. Mussel bed N:P excretion rates also increased as a function of overall community biomass at 15°C [$F_{(1,8)} = 6.274$, $R^2 = 0.473$, $P = 0.041$], 25°C [$F_{(1,8)} = 12.408$, $R^2 = 0.693$, $P = 0.010$], or 35°C [$F_{(1,8)} = 7.294$, $R^2 = 0.510$, $P = 0.031$; Fig. 4].

Mussel bed water column clearance rates decreased as a function of *A. ligamentina* relative biomass in the mussel bed at 15°C [$F_{(1,8)} = 6.023$, $R^2 = 0.462$, $P = 0.044$], 25°C [$F_{(1,8)} = 7.380$, $R^2 = 0.513$, $P = 0.030$], and 35°C [$F_{(1,8)} = 2.758$, $R^2 = 0.283$, $P = 0.141$; Fig. 4]. Although not statistically significant, increased relative biomass of *A. plicata* in the bed increased water column clearance rates at 15°C [$F_{(1,8)} = 0.250$, $R^2 = 0.001$, $P = 0.626$], 25°C [$F_{(1,8)} = 0.008$, $R^2 = 0.001$, $P = 0.930$], or 35°C [$F_{(1,8)} = 0.149$, $R^2 = 0.021$, $P = 0.711$]. Mussel bed water column turnover rates increased as a function of total biomass at all temperatures 15°C [$F_{(1,8)} = 17.621$, $R^2 = 0.716$, $P = 0.004$], 25°C [$F_{(1,8)} = 11.957$, $R^2 = 0.631$, $P = 0.011$], and 35°C [$F_{(1,8)} = 15.519$, $R^2 = 0.689$, $P = 0.006$; Fig. 4].

Discussion

Freshwater mussels are ectothermic filter feeders that naturally occur as dense, highly speciose assemblages. Their reliance on host fish for their larval stages, and trophic subsidies via benthic–pelagic coupling, make them important in stream ecosystems and a good model of overall stream ecosystem health. Our results demonstrate that mussel species co-occurring within the same communities (beds) have distinct physiological responses to stress that result in divergent contributions to ecosystem processes under varying environmental conditions. We found that co-occurring mussel species had different filtration, biodeposition, and nutrient excretion rates under different levels of thermal stress, and that these differences in ecosystem services were the direct result of different functional (i.e., physiological) traits. These trait-based responses indicate possible habitat limitations for mussel species as well as the potential magnitude and type of services they provide to the ecosystem (Table 1).

In addition, we detected at least two distinct thermal guilds. In our experiments, four species (*A. plicata*, *F. flava*, *M. nervosa*, and *O. reflexa*) were "thermally tolerant"; these species had their highest clearance and O_2 consumption rates at 35°C and were still assimilating energy at this temperature (anabolism > catabolism; Fig. 2). In contrast, the other four species (*A. ligamentina*, *L. cardium*, *T. truncata*, and *Q. pustulosa*) were "thermally

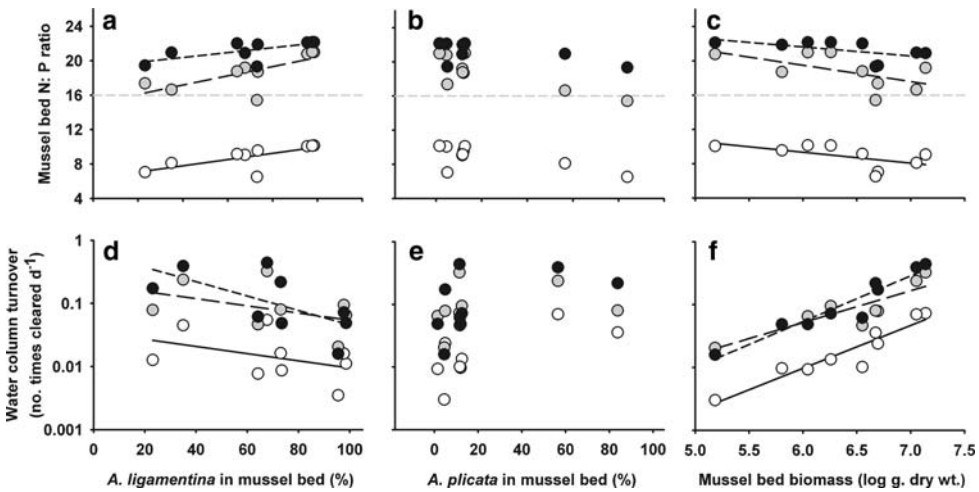

Fig. 4 Extrapolation of **a–c** nutrient excretion (mussel bed N:P ratio) and **d–f** clearance rate data (water column turnover) to mussel beds based on the percent of *Actinonaias ligamentina*, *Amblema plicata* and the total mussel bed biomass (log g dry wt). The *hatched line* represents the Redfield ratio. *Each point* represents a mussel bed experiencing a different temperature regime (*open circle* = 15°C, *gray filled circle* = 25°C, and *dark filled circle* = 35°C)

Table 1 Species-specific functional responses to experimental temperatures (25–35°C). Q_{10} Respiration rates, $A < C$ anabolism < catabolism, $A > C$ anabolism > catabolism

Species	Acquisition	Assimilation		Rendered ecological services				Functional group
	Clearance rate	O_2 consumption	Q_{10} (25–35°C)	Biodeposition	NH_3 excretion	P excretion	Molar N:P	
Actinonaias ligamentina	−	−	A < C	−	+	+	+	2a
Lampsilis cardium	−	=/−	A < C	−	+	+	+	2a
Quadrula pustulosa	+	+	A < C	+	+	+	−	2b
Truncilla truncata	=/−	−	A < C	+	−	+	−	2c
Amblema plicata	+	+	A > C	+	+	−	+	1
Fusconaia flava	+	+	A > C	+	+	=	+	1
Megalonaias nervosa	+	+	A > C	+	+	+	=	1
Obliquaria reflexa	+	+	A > C	+	+	=	+	1

sensitive"; these species decreased their clearance and O_2 consumption rates at 35°C and depleted energetic stories via anaerobic mechanisms (anabolism < catabolism; Table 1). These results are consistent with work performed by Baker and Hornbach 2001, who found seasonal differences in biochemical composition between *A. ligamentina* and *A. plicata* in the St Croix River, Minnesota. All species used in our experiments (and indeed the entire 297 species in the family Unionidae) are considered to belong to the same "functional group" of filter-feeding bivalves (Vaughn and Hakenkamp 2001). Our results illustrate that although all these species are considered "filter feeders", their optimal performance differs along a thermal continuum creating functional groups nested within the broader "filter feeder" guild.

Ectotherms are expected to increase performance with increasing temperature, and the thermally tolerant guild did this. With increasing temperature, *A. plicata*, *M. nervosa*, *F. flava,* and *O. reflexa* increased their clearance, biodeposition, and nutrient excretion rates, and had a greater impact on the surrounding ecosystem by increasing the rate and magnitude of energy and nutrient transfer from the water column to the sediment (Fig. 5; Table 1). In contrast, species in the thermally sensitive guild varied in their response to warmer temperatures and contributions to ecosystem services. *A. ligamentina* and *L. cardium* experienced thermal stress somewhere between 25 and 35°C as demonstrated by decreased assimilation rates. Their decreased filtration and biodeposition rates subsequently resulted in reduced material transfer from the water column to the sediment. To compensate for reduced energy, these mussels catabolized biochemical reserves. This degradation of biomolecules affected the quantity (more NH_3) and quality (higher N:P ratio) of excreted nutrients. Such stress-mediated differences in nutrient excretion could have stoichiometric implications for the composition of benthic periphyton and macroinvertebrate communities at higher trophic levels. *T. truncata* decreased both clearance and biodeposition rates to a lesser extent than *A. ligamentina* or *L. cardium*, and may represent an intermediate functional type between the thermally sensitive and thermally tolerant species. *Q. pustulosa* had its highest clearance,

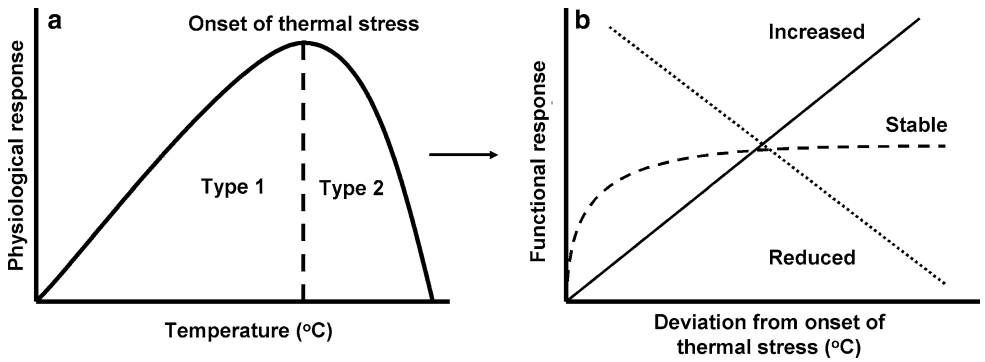

Fig. 5 Conceptual model of **a** physiological response to water temperature and **b** different functional responses of mussel species upon the onset of thermal stress. Mussels increase activity level (*Type 1*) up to the onset of thermal stress, at which point their functional contribution depends upon their physiological response (*Type 2*). These functional responses can result in: increased (*straight line*), stable (*dashed line*), and reduced (*dotted line*) benthic–pelagic coupling

biodeposition, and nutrient excretion rates at 35°C, but assimilation was low, resulting in higher biodeposition rates and greater benthic–pelagic coupling.

We integrated our lab-derived physiology information with field-collected community data to evaluate the importance of thermal regime, mussel community composition, and mussel functional traits on services provided to stream ecosystems. Stream temperatures in the south-central United States are highly variable, with summer extremes as high as 40°C during periods of extended drought (personal observation). Our extrapolation indicates that temperature significantly influences the N:P ratio of nutrients excreted by mussel communities with highest N:P ratios at 35°C and lowest at 15°C (Fig. 4). Species composition also influenced the quality of nutrients excreted by mussel communities. Thermally sensitive species excrete higher rates of NH_3 than tolerant species, and therefore contribute higher community N:P ratios. Conversely, mussel beds with greater relative abundance of thermally tolerant species excrete at lower N:P ratios (Fig. 4). McIntyre et al. (2007) compared random versus non-random extirpations in Lake African cichlids and found significant differences in community excretion rates associated with shifts in community structure. Our results suggest that losses of thermally sensitive mussel species will have similar effects on mussel community excretion. We realize that environmental variation under current climate scenarios is more dynamic; however, the point of our extrapolation is to demonstrate that the expressed traits within communities under these scenarios can have divergent (nutrient dynamics) and compensatory (benthic–pelagic coupling) effects on ecosystem function.

Interactive effects of temperature and nutrient regime have both stoichiometric and trophic implications in benthic foodwebs (Cross et al. 2006; Gafner and Robinson 2007). In our system, the magnitude of temperature and species composition influences on community nutrient excretion should be governed by local nutrient limitation. For example, mussel communities excreting above Redfield ratios (>16:1) should benefit periphyton with high N demand, while communities excreting below Redfield (<16:1) should benefit periphyton with high P demands (Hall et al. 2005). In a field experiment in the Kiamichi River, Oklahoma, with the same suite of species used in this study, Vaughn et al. (2007) found that *A. ligamentina* had strong effects on periphyton and macroinvertebrate assemblages in summer when it excreted high levels of NH_3 in this N-limited system (Spooner and Vaughn 2006; Vaughn et al. 2007) but no significant effects in fall when NH_3 excretion rates were reduced.

Shifts in temperature regimes and species dominance also influenced the nature of benthic–pelagic coupling (Fig. 5). Water column clearance rate extrapolations demonstrated that benthic–pelagic coupling declined with increased dominance of thermally sensitive species (*A. ligamentina*) but increased with greater dominance of thermally tolerant species (*A. plicata*). In general, mussel beds have lower clearance rates at 15°C, resulting in decreased benthic–pelagic coupling. However, unlike nutrient excretion, mussel beds have equal water column turnover rates at 25 and 35°C, resulting in similar benthic–pelagic coupling across temperatures.

Our results suggest that at elevated temperatures, mussel communities can have divergent effects on ecosystems for some ecosystem services (nutrient excretion) and compensatory effects for other services (benthic–pelagic coupling), which is highly relevant to conservation and current biodiversity ecosystem function theory. The ecological redundancy hypothesis posits that communities that contain ecologically similar species effectively behave as an insurance policy, maintaining ecosystem function in light of species decline. The mechanism of this hypothesis, density/biomass compensation, proposes that reductions of one species will be offset by increases of functionally similar species, such that the magnitude of ecosystem services is maintained (McGrady-Steed and Morin 2000; Yachi and Loreau 1999). This concept is likely not applicable to long-lived (5–100 years), slow-growing and late-maturing organisms (~4–5 years) such as unionid mussels (McMahon and Bogan 2001). Rather, our water column clearance extrapolation suggests that unionids, and perhaps other organisms with similar life history traits, may use physiological compensation (shifts in species activity level) to account for species losses and/or declines in order to maintain ecosystem services. However, like density compensation, physiological compensation is highly dependent on the pool of species traits within a community and the nature of environmental heterogeneity.

The magnitude, periodicity, and duration of droughts are increasing in the southern Unites States and mean summer temperatures are predicted to increase by as much as 4°C over the next 50 years (IPCC 2001; Mulholland et al. 1997). Many mussel species are already experiencing temperatures in the upper end of their thermal tolerance zone in this region, thus these increased temperatures (and associated decreased precipitation) will likely profoundly influence mussel community structure and the resulting ecosystem services in rivers in this region. For example, we detected significant effects of temperature on the physiology and ecological services provided by mussels at 35°C, and we observed mortality of three of the thermally sensitive species at 37–38°C, indicating that these temperatures are their upper limits for survival and reproduction. We have already observed changes in mussel community structure that are linked to stream warming. Monitoring data for ten sites in the Kiamichi River show

that overall mussel abundance and species richness have declined over the past 17 years as water temperatures have increased, and that mussel beds once dominated by thermally sensitive species are now dominated by thermally tolerant species (H. S. Galbraith et al., unpublished data). Our results indicate that these changes in community composition will lead to changes in ecosystem function.

Studies linking species traits to biodiversity and ecosystem function have typically been performed in systems where there is significant variation in modes of resource acquisition. Our study demonstrates that physiological trait differences within a functional feeding group can lead to differences in community composition and ecosystem services provided. In addition, we show that both positive and negative physiological performance can have positive effects on the surrounding ecosystem. As species are increasingly threatened by climate change, greater emphasis should be placed on understanding the contribution of physiological stress to the integrity and functioning of ecosystems.

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