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Species' traits and environmental gradients interact to govern primary production in freshwater mussel communities

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We examined the effect of species identity on ecosystem function across an environmental gradient by manipulating the relative dominance of three freshwater mussel species with divergent thermal preferences in mesocosms across a temperature gradient (15, 25, 35°C). We measured a suite of individual performance (oxygen consumption, nutrient excretion) and ecosystem response metrics (community, water column, benthic gross primary production and nutrient concentrations) to determine if species performance across temperatures was governed by 1) physiological responses to temperature, 2) species interactions associated with dominant species, or 3) context-dependent species interactions related to temperature (interaction of 1 and 2). Our results demonstrate that environmental context (temperature) combined with the functional traits of dominant species interactively influence the performance and services provided by other species, and that these shifts can have heightened effects on multiple compartments within an ecosystem. Therefore, in addition to declines in species richness, shifts in community dominance also should be considered when interpreting the effects of anthropogenic disturbances on the structure and functioning of ecosystems.

Experiments manipulating effects of biodiversity on ecosystem function (BEF) have led to proposed explanatory mechanisms including complementarity (niche complementarity and facilitation), functional redundancy, and species identity (Tilman 1999, Naeem and Wright 2003); all of which can operate concurrently (Cardinale et al. 2002, Hooper et al. 2005). The role of species identity confounds the interpretation of biodiversity experiments due to the 'sampling effect', i.e. the greater probability of selecting a species with disproportional traits that match the environmental landscape in higher richness treatments (Huston 1997). While studies have addressed the relative impact of unique species versus combined effects of entire assemblages, an important remaining question is whether the importance of unique species stems from their singular contribution to ecological processes or through the increased performance of other species in the community through facilitative or competitive interactions (Fridley 2001, Stachowicz 2001).

Furthermore, to extrapolate the effects of climate change and other anthropogenic disturbances to ecosystems, we also need to understand how community functional contributions change along environmental gradients (Hooper and Vitousek 1997). However, which mechanisms (i.e. complementarity or species identity) are operating depends on variation in species traits within a community, and the degree to which they match the local environment (Cardinale et al. 2002). Within communities, species vary in abundance, evenness and dominance. Species with optimal physiological performance under particular environmental conditions acquire and assimilate resources most efficiently, resulting in numerical or biomass dominance (Wilson and Keddy 1986). This link between performance, dominance and community structure has been associated with species distributions (Root 1988), grassland successional patterns (Grime 1987), and competitive interactions along resource gradients (Bestelmeyer 2000). In addition to elevated performance, dominant species may influence others through facilitation and competition (Jonsson and Malmqvist 2003, Smith et al. 2004). Although understanding the loss of function associated with species extinctions is important, shifts in species dominance within communities may have equal or even more severe ecological consequences (Ogutu-Ohwayo 1990, Symstad et al. 1998).

For the purpose of clarity, here we make an important distinction between terminologies used to describe the significance of species on the functioning of ecosystems: 1) species performance (hereafter referred to as performance), which denotes the physiological condition or health of a particular species within a community, these metrics often pertain to how organisms respond to a stressor or species interaction (i.e. who is winning?). 2) Species ecosystem service (hereafter referred to as ecosystem service), which describes the particular service that a species confers to an ecosystem (e.g. nutrient excretion, filtration rate); and 3) ecosystem process, which describes an underlying process inherently important to the functioning of ecosystems (primary production, nutrient retention). This distinction is important, because often

the species performance and ecosystem service variables (species-specific change in biomass within treatments) are nested within the ecosystem process variable (primary production) making it difficult to assess how species interactions truly influence ecosystem processes.

More recently, the complexity of BEF experimental designs have expanded to include horizontal and vertical diversity (primary producers, secondary and tertiary consumers, and decomposers) across a variety of systems (marine, terrestrial and aquatic) and processes (nutrient cycling, decomposition and primary production) (Cardinale et al. 2009). For the most part, these studies are beginning to incorporate metrics of ecosystem processes that are independent of those of species performance or services. Not surprisingly, the ecological interpretations of such studies are quite complex with a limited mechanistic understanding of how species-specific trait expression and consequent species interactions influence ecosystem processes, especially with respect to environmental contexts (but see Cardinale et al. 2009).

Freshwater mussel (Bivalvia, Unionoida; hereafter 'mussels') communities are a good system for examining hypotheses linking physiology, species interactions, and species dominance effects on ecosystem processes. Mussels are a guild of long-lived (6–100 years), benthic, burrowing, filter-feeders that occur as speciose aggregations (mussel beds) that can dominate benthic biomass in eastern North American rivers (Vaughn and Spooner 2006). Nutrient mineralization via mussel excretion facilitates benthic algal growth, an important subsidy in nutrient-limited streams (Vanni 2002, Vaughn et al. 2007, Christian et al. 2008). This subsidized periphyton increases macroinvertebrate abundance by providing biogenic structure and food resources (Spooner and Vaughn 2006). The magnitude of mussel effects on benthic communities varies with environmental conditions; strongest effects occur under low flow and high water temperature (Spooner and Vaughn 2006, Vaughn et al. 2007).

Mussels are thermo-conformers that passively adjust their metabolism to ambient temperatures (McMahon and Bogan 2001) and can be assigned to guilds based on their temperature-specific functional performance (Spooner and Vaughn 2008). Thermally tolerant species have increased resource assimilation and higher ecosystem process rates at warm temperatures (e.g. nutrient excretion, filtration and biodeposition), while thermally sensitive species have decreased assimilation rates and display an array of functional responses including increased/decreased filtration, biodeposition and nutrient excretion rates. Species from both guilds co-occur in natural assemblages, but can alternate in dominance (Spooner 2007).

Here we artificially recreate conditions relevant to dominance or sampling effects by holding richness constant and examining how both ecological processes and species interactions change when 1) all traits are present in the community but vary in their dominance; 2) occur under different environmental contexts (temperature) that are relevant to the expression of thermal traits. Because mussels influence multiple trophic levels through their filtering, burrowing, and excretion activities (hereafter referred to as ecosystem services), we can make estimates of consequent ecosystem processes (primary production) that are independent of measures of species performance (mussel body condition index, mass-specific oxygen consumption) or their services (nutrient excretion). We performed manipulative experiments to test the following hypotheses: 1) physiology governs the performance of species, their contributed ecological services, and subsequent processes with the ecosystem. Thus, the relative contributions of mussel species within communities to ecological processes are constrained by their physiological responses to temperature (Fig. 1a). 2) Species interactions govern the performance of species, their contributed services, and subsequent processes within ecosystem. In other words, dominant species influence the condition and services provided by other mussel species in the community by increasing (facilitation) or decreasing (competition) their performance (Fig. 1b). 3) Species physiology and interactions, and thus ecosystem processes are governed by species interactions under specific environmental conditions (Fig. 1c).

Material and methods

Experimental design

We manipulated species dominance of a subset of a natural mussel assemblage from the Little River, OK, a well-studied river with healthy, diverse mussel assemblages (Spooner 2007, Galbraith et al. 2010). We held species richness and total density constant to evaluate the relative contribution of species to ecosystem processes when all known species traits were present in the community. We selected five common species that co-occur in this river, but that have different physiological responses to thermal stress resulting in potentially different ecosystem services (nutrient excretion rates) and ecosystem processes (primary production) (Spooner and Vaughn 2008). *Actinonaias ligamentina* (244.94 mm mean shell length $\pm$ 9.21) and *Quadrula pustulosa* (57.26 $\pm$ 3.98) are thermally sensitive species that catabolyze energy reserves at warm temperatures. *Amblema plicata* (202.5 $\pm$ 9.90), *Megalonaias nervosa* (406.2 $\pm$ 30.85) and *Obliquaria reflexa* (45.48 $\pm$ 2.53) are thermally tolerant species that continue to assimilate energy at warm temperatures (Spooner 2007). In each mesocosm, we manipulated the numerical relative abundance of *A. ligamentina*, *A. plicata* and *Q. pustulosa* to reflect varying degrees of community biomass dominance (41, 23, 18, 12 and 6%) (Appendix 1 Table A1). We placed the two remaining species in treatments to maintain an orthogonal design and ensure equal representation for the three dominant species (Appendix 1 Table A1). Correlation of species biomass across mesocosms revealed that assigned dominance treatments were independent of one another (Appendix 1 Table A2).

We used a replicated ANCOVA design under three temperature regimes (15, 25, 35°C) in 14 (12 treatment and two control) re-circulating stream mesocosms (1.5 m height $\times$ 0.5 m width $\times$ 0.5 m depth). Each mesocosm contained 17 mussels (23 individuals m^{-2}). Experiments were performed as three separate runs (one per temperature). Mesocosms consisted of a molded plastic liner suspended inside a fiberglass basin (Allen and Vaughn 2009) and filled to 15 cm depth with pea-sized gravel. Mesocosm conditions were maintained with 110 l of conditioned well water, 12 h light/dark photoperiod, and constant flow of 15 cm s^{-1} with a 1/32

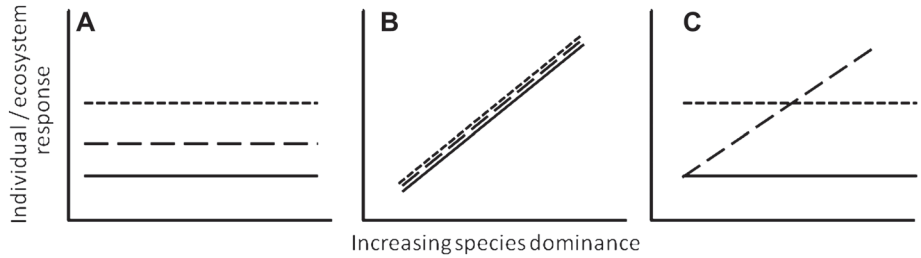

Figure 1. Hypothetical relationships between species dominance and temperature manipulations: (A) Physiology hypothesis: Performance and environmental variables are governed by strict physiology, (B) Interactions hypothesis: Performance and environmental variables are governed by species interactions; (C) Context-dependent interactions hypothesis: Performance and environmental variables are governed by species interactions at specific temperatures. Solid lines represent response variable at 15°C, long dashed lines represent response variable at 25°C, short dashed lines represent response variable at 35°C.

horsepower pump. Twelve porous silica disks (2.5 cm^2) were placed in each mesocosm for periphyton colonization.

Mussels were acclimated to experimental temperatures for two weeks and fed a mixed algal assemblage ad libitum. Twenty-four hours before each experimental run, we brushed biofilm from mussel shells, marked individuals with a numbered tag (Vaughn et al. 2007), and measured length and wet weight. Mussels were placed in separate holding tanks at experimental temperatures and not fed for 24 h to ensure gut evacuation. Mussels were then randomly selected from each acclimation tank and assigned to treatments. Dry-mass of individuals was calculated using species-specific wet mass-dry mass regressions, which allowed us to account for differences in size, internal cavity water volume, and mesocosm biomass without sacrificing mussels. Each mesocosm was fed 500 ml of concentrated, cultured, mixed-algal assemblage daily (0.02 mg chl a l^{-1}). Each experimental run lasted two weeks. Following the experiment, mussels were returned alive to the river.

Mussel response variables

Ecological services (nutrient excretion) and mussel performance (oxygen consumption, condition index) of individual mussels were quantified on the last day of each experimental run. For each mesocosm, three replicate individuals of each species were sampled with the exception of certain treatments where only one or two individuals of those species were represented. Individuals were gently scrubbed clean and placed in 1-l plastic containers with filtered water, two 10 ml water samples (for ammonia and phosphorus excretion) were collected, and initial DO was measured. Containers were incubated in a water bath at experimental temperatures for one hour, then two more 10 ml water samples were collected, final DO was recorded, and mussel wet weight was measured.

Phosphorus was quantified using the ascorbic acid method with persulphate digestion, and ammonia was quantified with the phenate method (ASDM 1996). Excretion rates were calculated as the net difference in initial and final nutrient concentrations corrected for nutrient evolution in control treatments, and standardized for container volume, incubation time and mussel biomass. Molar N:P ratios (nitrate:phosphate) were calculated as moles of nitrogen divided by moles of total phosphorus.

Oxygen consumption was calculated as the net difference in oxygen depletion between initial and final measurements, corrected for controls and standardized for container volume, incubation time and mussel dry weight. In addition, we non-lethally assessed body condition by calculating a condition index as the change in mass corrected for length for each individual from the beginning to the end of the experiment. Mean values for each species were calculated for all response variables within a mesocosm and treated as a replicate, therefore each species had a sample size of 12.

Ecosystem process variables

Water column nutrient flux

On days 1, 4, 9 and 14, we collected 125 ml of water from each mesocosm for total phosphorous and nitrate analysis. Nutrient concentrations were determined colorimetrically using the ascorbic acid method with persulfate digestion for total phosphorous (TP), and the cadmium reduction technique for nitrate (NO_3^-) (ASDM 1996), and corrected for mesocosm mussel biomass (dry weight). To estimate the extent to which nutrients accrued in the mesocosms over time (nutrient flux), we performed a regression for each nutrient (total phosphorus and nitrate) with time as the independent variable. We also calculated the molar N:P of the water column at the end of each run (day 14) to determine final nutrient conditions with respect to temperature and species dominance.

Multi-compartment estimates of gross primary production

All estimates of gross primary production were performed on the last day of each experimental run (day 14). We measured water column gross primary production (WCGPP) with 1 l water samples individually collected in airtight glass containers from each mesocosm. We measured dissolved oxygen with a Hach LDO HQ_{10} meter ($\pm$0.01 mg l^{-1}); we incubated each container in the dark in an enclosed water bath at experimental temperatures for 1.5 h and then re-measured DO. Containers were then incubated in the light at experimental temperatures for an additional 1.5 h, when final DO was measured and recorded. The contents of each container were filtered with a GF/F filter, wrapped in foil, and frozen for subsequent chlorophyll a determination via acetone extraction (ASDM 1996). WCGPP was calculated as the

sum of oxygen production during light incubation plus respiration during the dark incubation, corrected for incubation time, water volume, chlorophyll a concentration and mussel community biomass (dry weight).

Benthic gross primary production (BGPP) was estimated by collecting two replicate silica disks from each mesocosm, and placing them in airtight 125 ml glass containers containing filtered water held at experimental temperatures. BGPP estimates were calculated with the water bath procedure described above, after which silica disks were wrapped in foil and frozen for chlorophyll a determination. BGPP was calculated as above, correcting for incubation time, chlorophyll a concentration, disk surface area, and mesocosm mussel biomass (dry weight).

Estimates of community (entire mesocosm) gross primary production were performed on the final day of each run. Mesocosm pumps were turned off and replaced with low-velocity aquarium pumps to allow water circulation with minimal turbulence. Dissolved oxygen (DO) concentrations were measured with a Hach LDO meter (± 0.01 mg l^{-1}), mesocosms were left in the dark for an hour and DO re-measured, mesocosms were left in the light for one hour, a final DO measurement was taken, and mesocosm pumps were turned back on. Community gross primary production (CGPP) was calculated similar to WCPP and BGPP correcting for time, algal abundance (chlorophyll a), and mussel community biomass (dry weight).

Data analyses

For each mesocosm the relative proportion of each dominant species (*Actinonaias*, *Amblema* and *Quadrula*) was determined by dividing the total dry mass of each species by the total dry mass in the mesocosm. We modeled individual and ecosystem level responses to temperature and species dominance (*Act*, *Amb*, *Quad*) manipulations as follows:

$$(a)\ EV_i \text{ or } PV_i = \beta_0 + \beta_1 (Temp) + \beta_2 (ActDom) + \beta_3 (Temp \times ActDom) + \varepsilon_i$$

$$(b)\ EV_i \text{ or } PV_i = \beta_0 + \beta_1 (Temp) + \beta_2 (AmbDom) + \beta_3 (Temp \times AmbDom) + \varepsilon_i$$

$$(c)\ EV_i \text{ or } PV_i = \beta_0 + \beta_1 (Temp) + \beta_2 (QuadDom) + \beta_3 (Temp \times QuadDom) + \varepsilon_i$$

Where EV_i and PV_i respectively represent environmental (BGPP, WCGPP, CGPP) and individual performance (excretion, oxygen consumption and condition) response variables; *Temp* represents the mesocosm temperature manipulation (15, 25, 35°C); *(species)Dom* represents the relationship of the response variables with increased dominance; and *Temp* × *(species)Dom* represents the interaction between increased dominance and temperature manipulation. β_o and ε_i respectively represent the intercept and error terms of the model.

We used a generalized linear model approach to construct and evaluate the above models in the following order. First we compared the Akaike information criterion (AIC), to evaluate which species model (a, b or c above) best approximated the variation in species performance or environmental response. We then evaluated which parameter estimate was most relevant to the response variable (*Temp*, *(species)Dom*, *Temp* × *(species)Dom*). For example, if the response variables were largely driven by temperature and less by the effect of species dominance or interaction of the two, we would expect a larger, significant, test statistic (Wald's χ^2) for the *Temp* parameter estimate (Fig. 1a). We then evaluated the nature of *Temp* × *(species)Dom* interaction by performing a separate slopes analysis, which tests the null hypothesis that the slope of the relationship between a particular species dominance and response variable (performance or environmental) at a given temperature is zero. All generalized linear models were performed with an assumed normal error distribution for dependent variables and an identity link function using SPSS software (SPSS 2001).

Results

Species performance

With the exception of the *Amblema* model, which best approximated variation in *Amblema* oxygen consumption rates, the *Actinonaias* model consistently had the lowest AIC values, and therefore best described the variation in oxygen consumption rates for the remaining species *Actinonaias*, *Megalonaias*, *Obliquaria* and *Quadrula* (Fig. 2, Appendix 1 Table A3). Furthermore, in the case of *Actinonaias* oxygen consumption rates, and the *ActDom* × *Temp* interaction effects for the remaining species (*Megalonaias*, *Obliquaria* and *Quadrula* oxygen consumption rates) had greater parameter test statistics (Wald's χ^2) compared to *Temp,* indicating that species interactions may be more important than strict physiology in governing oxygen consumption rates (Fig. 2, Appendix 1 Table A3). Of these *ActDom* × *Temp* interactions, increased *Actinonaias* dominance resulted in decreased oxygen consumption rates at 25°C for *Megalonaias* ($\chi^2 = 6.4$, $\beta = -0.018$, $p = 0.012$) and *Obliquaria* ($\chi^2 = 6.0$, $\beta = -0.024$, $p = 0.018$) and increased oxygen consumption for *Actinonaias* ($\chi^2 = 25.7$, $\beta = 0.078$, $p < 0.001$)(Fig. 2, Appendix 1 Table A3). Conversely, increased *Actinonaias* dominance also increased oxygen consumption rates at 35°C for *Megalonaias* ($\chi^2 = 17.6$, $\beta = 0.003$, $p < 0.001$), *Obliquaria* ($\chi^2 = 23.9$, $\beta = 0.124$, $p < 0.001$) and *Quadrula* ($\chi^2 = 6.5$, $\beta = 0.186$, $p = 0.011$) species (Fig. 2, Appendix 1 Table A3).

The *Actinonaias* model also resulted in the lowest AIC values for all species' body condition indices. However, the model parameter test statistics were greatest for *Temp* for both *Amblema* and *Quadrula*, yet were highest for *ActDom* × *Temp* for the remaining three species (*Actinonaias*, *Obliquaria* and *Megalonaias*). Body condition was negatively associated with increased *Actinonaias* dominance at 35°C (*Actinonaias*: $\chi^2 = 14.5$, $\beta = -0.106$, $p < 0.001$, *Amblema*: $\chi^2 = 3.2$, $\beta = -0.055$, $p = 0.044$, *Obliquaria*: $\chi^2 = 11.8$, $\beta = -0.016$, $p < 0.001$, *Quadrula*: $\chi^2 = 5.0$, $\beta = -0.017$, $p = 0.03$) for all species except *Megalonaias,* which was positively associated with *Actinonaias* dominance at 25°C $\chi^2 = 13.3$, $\beta = 0.116$, $p < 0.001$ (Appendix 1 Table A3).

Species ecosystem service (nutrient excretion)

The *Actinonaias* model had the lowest AIC values for all species' ammonia excretion rates. In addition, the

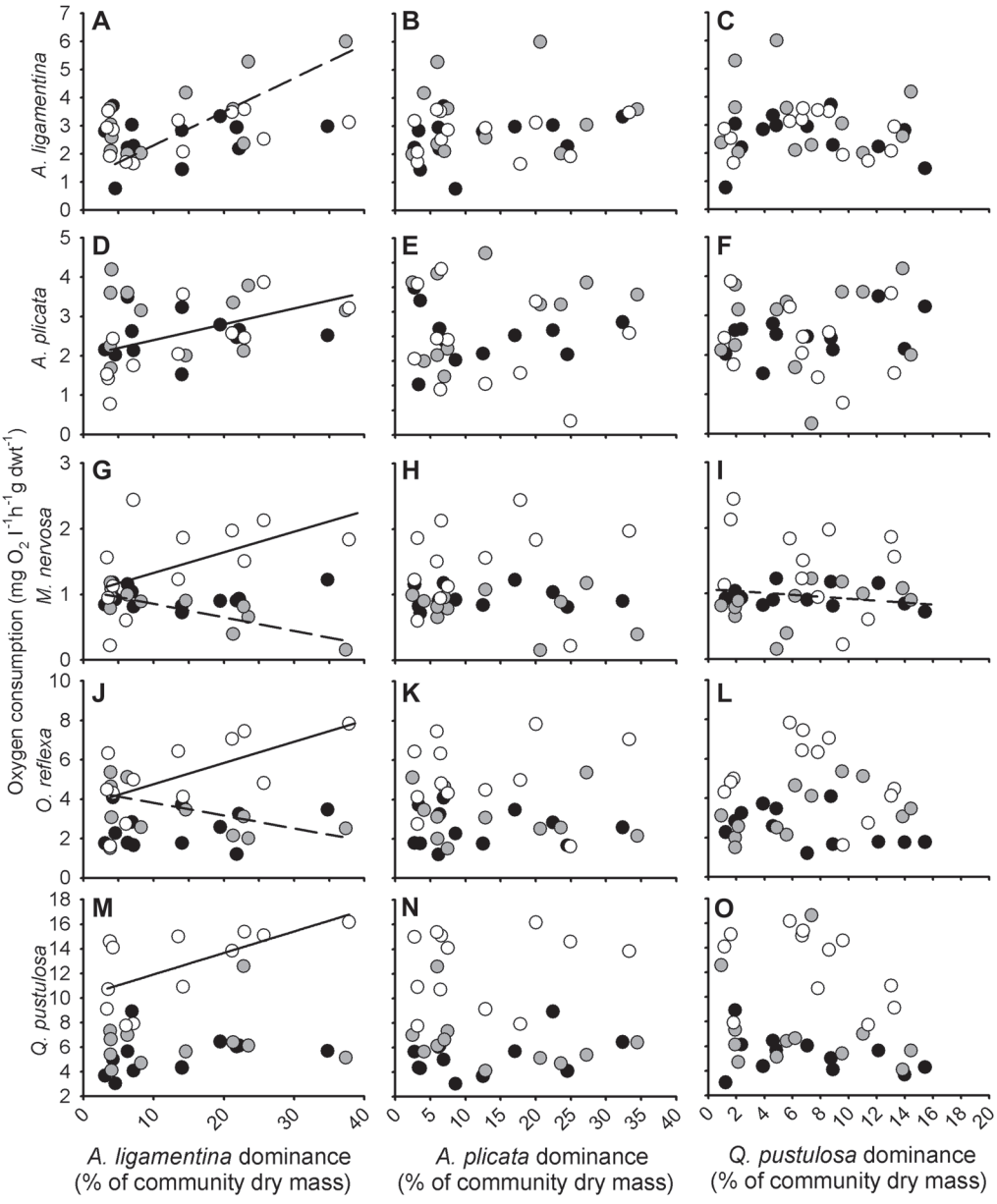

Figure 2. Effect of relative species dominance (*A. ligamentina*, *A. plicata*, and *Q. pustulosa*) on the mean oxygen consumption rates of (A–C, *A. ligamentina*), (D–F, *A. plicata*), (G–I, *M. nervosa*), (J–L, *O. reflexa*), and (M–O, *Q. pustulosa*). Dark circles = 15°C, grey circles and dashed lines = 25°C, and white circles and solid lines = 35°C.

interaction parameter *ActDom* × *Temp* had the largest test statistic compared to *Temp* or *ActDom* indicating that mussel excretion rates are governed by context-dependent species interactions. All ammonia excretion rates were positively related to *Actinonaias* dominance at 35°C [*Actinonaias*: $\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$, *Amblema*: $\chi^2 = 21.6$, $\beta = 0.140$, $p < 0.001$, *Megalonaias*: $\chi^2 = 19.1$, $\beta = 0.066$, $p < 0.001$; *Obliquaria*: $\chi^2 = 19.8$, $\beta = 0.326$, $p < 0.001$, *Quadrula*: $\chi^2 = 11.2$, $\beta = 0.223$, $p < 0.001$ (Fig. 3, Appendix 1 Table A3)].

Conversely, no consistent species dominance model explained phosphorus excretion rates. For example, the *Actinonaias* model had the lowest AIC scores for *Amblema*, *Megalonaias* and *Obliquaria* phosphorus excretion rates, while the *Amblema* model had the lowest AIC scores for *Quadrula*, and the *Quadrula* model for *Actinonaias* phosphorus excretion rates. Not surprisingly, the *Temp* parameter test statistic for all species phosphorus excretion models was greater than those of the species dominance or interaction parameters indicating that physiological mechanisms associated with temperature, rather than species interactions, govern phosphorus excretion. Nonetheless, despite non-significant interaction parameters, significant relationships did arise at 15°C, where almost all species phosphorus excretion rates negatively related to *Act*, *Amb* and *Quad* dominance (Appendix 1 Table A3). At 25°C, *Obliquaria* phosphorus excretion was positively associated with both *Amblema* (*Obliquaria*: $\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) and *Actinonaias* dominance (*Obliquaria*: $\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) and *Quadrula* phosphorus excretion was negatively

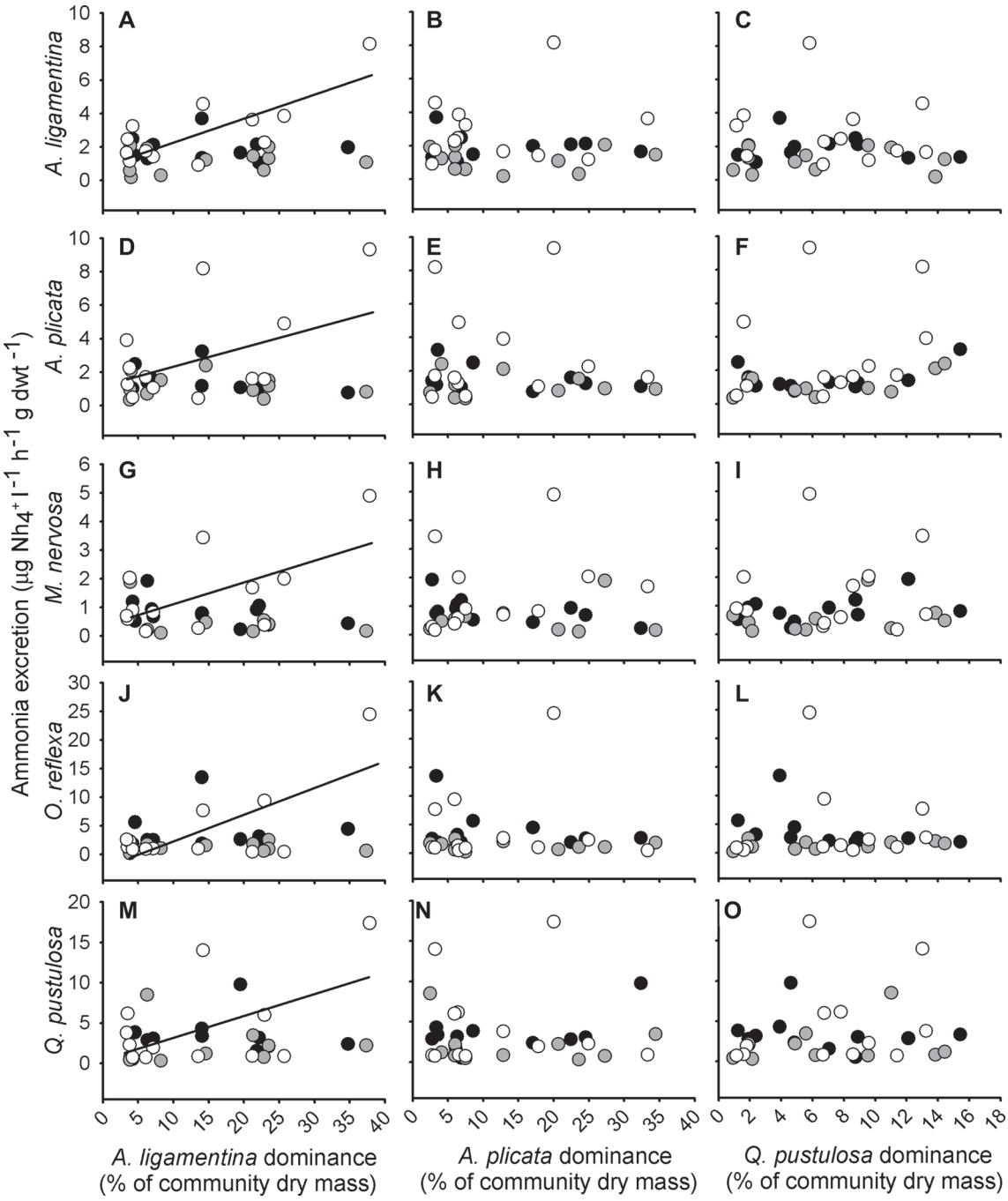

Figure 3. Effect of relative species dominance (*A. ligamentina*, *A. plicata*, and *Q. pustulosa*) on the mean ammonia excretion rates of (A–C, *A. ligamentina*), (D–F, *A. plicata*), (G–I, *M. nervosa*), (J–L, *O. reflexa*), and (M–O, *Q. pustulosa*). Dark circles = 15°C, grey circles and dashed lines = 25°C, and white circles and solid lines = 35°C.

associated with *Actinonaias* dominance (*Quadrula*: $\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$)(Appendix 1 Table A3).

Mussel N:P excretion models were also erratic, largely due to the dependence of ammonia excretion on species interactions and phosphorus excretion on temperature related mussel physiology. For example, the *Quadrula* model had the lowest AIC value for *Amblema* N:P ratios and the *Amblema* model had the lowest AIC values for *Megalonaias* N:P ratios (Appendix 1 Table A3). The *Actinonaias* model had the lowest AIC values for *Actinonaias*, *Quadrula* and *Obliquaria* N:P excretion ratios. As such, the *Temp* parameter test statistic was greatest for *Actinonaias*, *Amblema* and *Megalonaias* models, while the *ActDom* parameter test statistic was greatest for *Obliquaria* and *Quadrula* N:P excretion models (Appendix 1 Table A3). The influence of interaction terms reflected both ammonia and phosphorus species interactions with strong effects of *Quadrula* dominance on *Actinonaias* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$), *Amblema* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$), *Megalonaias* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) and *Obliquaria* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) N:P ratios at 15°C and strong effects of *Actinonaias* dominance on *Actinonaias* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$), *Megalonaias*

($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$), *Obliquaria* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) *and Quadrula* ($\chi^2 = 43.2$, $\beta = 0.128$, $p < 0.001$) N:P ratios at 35°C.

Environmental variables

Actinonaias models had the lowest AIC values for water column nitrate accrual, phosphorus accrual and standing crop N:P ratios (Table 1). Furthermore, *ActDom* × *Temp* had the largest parameter test statistic for nitrate accrual, *ActDom* for phosphorus accrual, and *Temp* for water column N:P ratio (*Temp*) indicating that water column nitrogen and phosphorus accrual may be governed by context-dependent species interactions involving *Actinonaias* dominance, yet N:P ratios at the end of the experiment appeared to be governed solely by water temperature (Table 1). For example water column nitrate and phosphorus accrual over time were both strongly positively related to *ActDom* at 35°C (Fig. 4, Table 1). Interestingly, although the interaction parameter test statistic was non-significant, water column N:P ratios at the end of the experiment were negatively related to *ActDom* at 15°C and positively related to *ActDom* at 25°C and 35°C (Fig. 4, Table 1).

Table 1. Results of generalized linear model explaining the effects of temperature and species dominance manipulations. Slope parameter estmates in parentheses. Significant p-values in bold.

		Actinonaias		*Amblema*		*Quadrula*	
Response variable	Paramater	$x^2_{(DF)}$	p-value	$x^2_{(DF)}$	p-value	$x^2_{(DF)}$	p-value
	Full model	34(30) AIC =−258.6	**<0.001**	$34_{(30)}$ AIC =−249.8	**<0.001**	$34_{(30)}$ AIC =−238.9	**<0.001**
	Temp	$6.72_{(2)}$	**0.035**	$9.1_{(2)}$	**0.01**	$9.3_{(2)}$	**0.009**
	Dominance	ll–$2_{(1)}$	**0.001**	$6.5_{(1)}$	**0.011**	$0_{(1)}$	0.978
Nitrogen	Temp×Dom	13–$7_{(2)}$	**0.001**	$1.2_{(2)}$	0.438	$0.7_{(2)}$	0.714
	15×Dom	$0.1_{(1)}$ (B=0.000)	0.722	$0.2_{(1)}$ (B=0.000)	0.637	$1.1_{(1)}$ (B=−0.001)	0.371
	25×Dom	$2.0_{(1)}$ (B=−0.001)	0.157	$2.2_{(1)}$ (B=−0.001)	0.138	$3.1_{(1)}$ (B=−0.004)	0.061
	35×Dom	$87.5_{(1)}$ (B=0.007)	**<0.001**	$4.25_{(1)}$ (B=0.001)	0.084	$3.4_{(1)}$ (B=0.001)	0.059
	Full model	$34_{(30)}$ AIC =−379.6	**<0.001**	$34_{(30)}$ AIC =−373.6	**<0.001**	$34_{(30)}$ AIC =−371.6	**<0.001**
	Temp	0–$9_{(2)}$	0.646	$0.68_{(2)}$	0.711	$0.4_{(1)}$	0.804
	Species	$11_{(1)}$	**0.001**	$2.6_{(1)}$	0.232	$2.4_{(1)}$	0.123
Phosphorus	Temp×Dom	$2.4_{(2)}$	0.306	$1.1_{(2)}$	0.572	$1.0_{(1)}$	0.604
	15×Dom	$3.6_{(1)}$ (B=0.001)	0.062	$2.1_{(1)}$ (B=0.001)	0.134	$2.9_{(1)}$ (B=0.001)	0.183
	25×Dom	$3.1_{(1)}$ (B=0.000)	0.083	$1.1_{(1)}$ (B=0.000)	0.296	$0.7_{(1)}$ (B=0.000)	0.387
	35×Dom	$6.0_{(1)}$ (B=0.002)	**0.014**	$1.9_{(1)}$ (B=0.000)	0.171	$0.7_{(1)}$ (B=0.000)	0.413
	Full model	$34_{(30)}$ AIC =38.5	**<0.001**	$34_{(30)}$ AIC =48.1	**<0.001**	$34_{(30)}$ AIC =53.3	**<0.001**
	Temp	$20.6_{(2)}$	**<0.001**	$29.9_{(2)}$	**<0.001**	$29.9_{(2)}$	**<0.001**
	Species	$10.9_{(1)}$	**0.001**	$l.l_{(1)}$	0.29	$3.6_{(1)}$	0.057
N:P	Temp×Dom	$3.6_{(2)}$	0.166	$3.1_{(2)}$	0.223	$0.8_{(2)}$	0.655
	15×Dom	$11.9_{(1)}$ (B= 0.179)	**0.001**	$1.49_{(1)}$ (B=−0.048)	0.224	$2.3_{(1)}$ (B=−0.079)	0.109
	25×Dom	$9.2_{(1)}$ (B=0.153)	**0.002**	$1.4_{(1)}$ (B=0.074)	0.231	$0.2_{(1)}$ (B=−0.041)	0.672
	35×Dom	$45.7_{(1)}$ (B=0.341)	**<0.001**	$4.9_{(1)}$ (B=0.082)	0.066	$2.2_{(1)}$ (B=0.194)	0.113
	Full model	$34_{(30)}$AIC =−224.1	**<0.001**	$34_{(30)}$ AIC =−193.7	**<0.001**	$34_{(30)}$AIC =−193.2	**<0.001**
	Temp	20.1_{C}j	**<0.001**	$20.7_{(2)}$	**<0.001**	$11.9_{(2)}$	**0.003**
	Species	$0.6_{(fl)}$	0.422	$27.7_{(1)}$	**<0.001**	$0.5_{(1)}$	0.536
Benthic GPP	Temp×Dom	$0.4_{(2)}$	0.817	$23.2_{(2)}$	**<0.001**	$0.9_{(1)}$	0.88
	15×Dom	$24.6_{(1)}$ (B=−0.012)	**<0.001**	$9.7_{(1)}$ (B=−0.005)	**0.002**	$4.6_{(1)}$ (B=−0.012)	0.088
	25×Dom	$0.0_{(1)}$ (B=0.000)	0.871	$22.5_{(l)}$ (B=0.007)	**<0.001**	$2.2_{(1)}$ (B=0.005)	0.137
	35×Dom	$2.1_{(1)}$ (B=0.005)	0.092	$82.9_{(1)}$ (B=0.015)	**<0.001**	$3.9_{(1)}$ (B=0.013)	0.109
	Full model	$34_{(30)}$AIC =−169.9	**<0.001**	$34_{(30)}$A1C =−157.4	**<0.001**	$34_{(30)}$ AIC =−156.9	**<0.001**
	Temp	2-$1_{(2)}$	0.35	$2.5_{(2)}$	0.288	$0.8_{(2)}$	0.67
	Species	8-$3_{(1)}$	**0.004**	$1.3_{(1)}$	0.252	$0_{(1)}$	0.927
Water column GPP	Temp×Dom	7-$4_{(2)}$	**0.024**	$0.4_{(2)}$	0.822	$l.3,_{2)}$	0.524
	15×Dom	$2.1_{(1)}$ (B=0.002)	0.449	$2.4_{(1)}$ (B=0.005)	0.124	$0.5_{(1)}$ (B=0.003)	0.498
	25×Dom	$11.1_{(1)}$ (B=0.007)	**0.001**	$0.1_{(1)}$ (B=-0.001)	0.765	$1.9_{(1)}$ (B=−0.006)	0.172
	35×Dom	$15.4_{(1)}$ (B=0.010)	**<0.001**	$3.3_{(l)}$ (B=0.006)	0.71	$0.4_{(1)}$ (B=0.003)	0.542
	Full model	$34_{(30)}$AIC=−91.8	**0.005**	$34_{(30)}$ AIC=-89.3	**0.005**	$34_{(30)}$ A1C=−81.8	**0.005**
	Temp	$1.2_{(2)}$	0.555	$0.2_{(2)}$	0.884	$2.6_{(2)}$	0.268
	Species	$9_{(1)}$	**0.003**	$11.8_{(1)}$	**0.001**	$0.7_{(1)}$	0.393
Community GPP	Temp×Dom	$03_{(2)}$	0.838	$1.5_{(2)}$	0.46	$0.4_{(2)}$	0.813
	15×Dom	$2.1_{(1)}$ (B=0.017)	0.154	$2.7_{(1)}$ (B=0.019)	0.091	$0.2_{(1)}$ (B=0.007)	0.634
	25×Dom	$l.8_{(1)}$ (B=0.011)	0.177	$2.8_{(1)}$ (B=0.013)	0.095	$0.0_{(1)}$ (B=−0.001)	0.927
	35×Dom	$19.4_{(1)}$ (B=0.036)	**<0.001**	$25.7_{(1)}$ (B=0.041)	**<0.001**	$2.6_{(1)}$ (B=0.031)	0.159

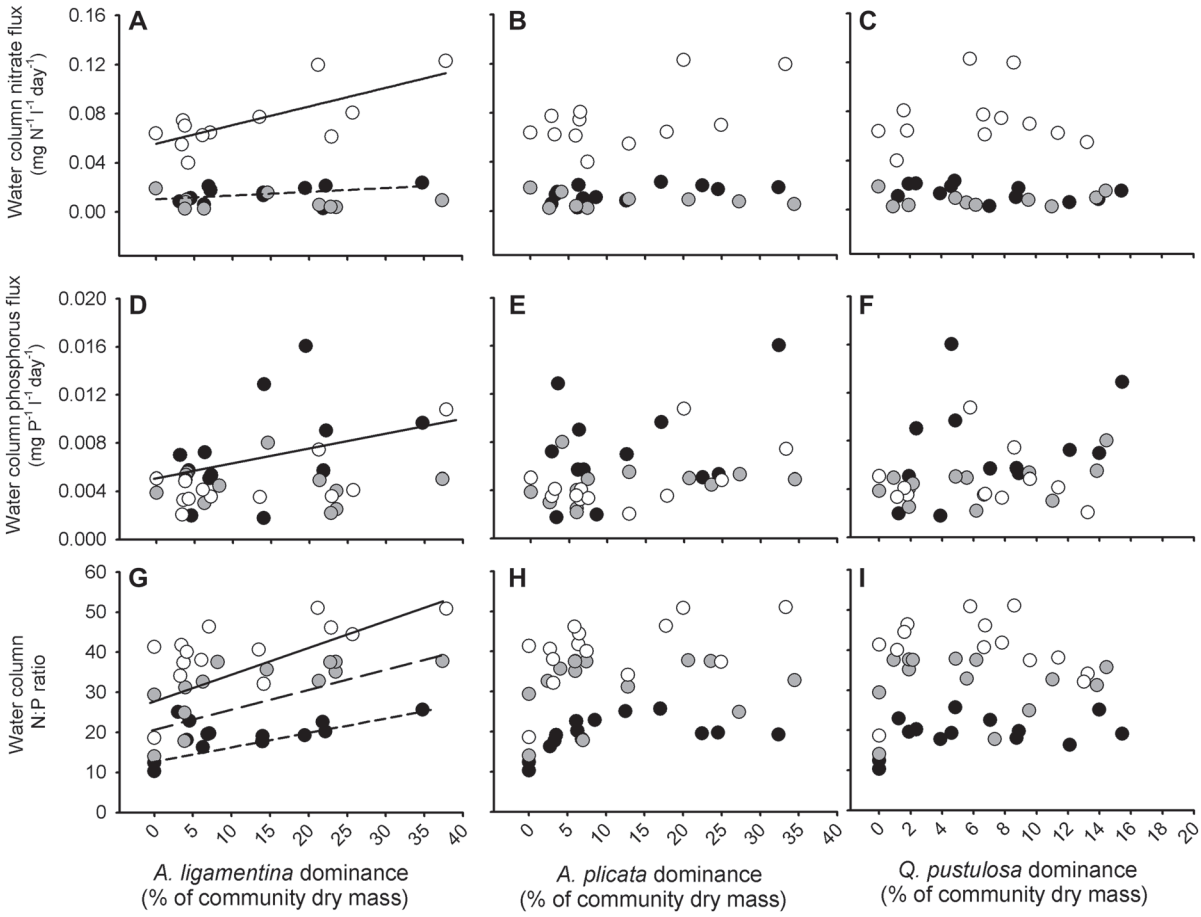

Figure 4. Relationship between water column nitrate flux and (A) percent *A. ligamentina* biomass, (B) percent *A. plicata* biomass, (C) percent *Q. pustulosa* biomass. Relationship between water column phosphorus flux and (D) percent *A. ligamentina* biomass, (E) percent *A. plicata* biomass, (F) percent *Q. pustulosa* biomass. Relationship between water-column N:P ratio of Day 14 and (G) percent *A. ligamentina* biomass, (H) percent *A. plicata* biomass, (I) percent *Q. pustulosa* biomass on day 14 Dark circles = 15°C, grey circles and dashed lines = 25°C, and white circles and solid lines = 35°C.

The *Amblema* model generated the lowest AIC value for BGPP. In addition, all parameter test statistics (*Temp*, *AmbDom* and *AmbDom* × *Temp*) within the *Amblema* model were significant, yet largest for *AmbDom* and *AmbDom* × *Temp* parameters (Table 1). The interaction between *AmbDom* and *Temp* resulted in a significant positive relationship between BGPP and *Amblema* dominance at 25 and 35°C (Fig. 5, Table 1). Both *ActDom* and *AmbDom* however, were negatively related to BGPP at 15°C (Fig. 5, Table 1). The *Actinonaias* model generated the lowest AIC value for WCGPP, and both the *ActDom* and *ActDom* × *Temp* parameter statistics were significant indicating that species interactions may govern WCGPP. For example, *ActDom* positively related to WCGPP at 25°C and 35°C (Fig. 5, Table 1).

While the *Actinonaias* model generated the lowest AIC value for CGPP, it wasn't much smaller than the *Amblema* model. For both species models, the *ActDom* and *AmbDom* parameter test statistics were largest and significant indicating that overall, CGPP increased as a function of both *Actinonaias* and *Amblema* dominance (Fig. 5, Table 1). Despite non-significant interaction terms for both models, *Actinonaias* and *Amblema* dominance both were positively associated with CGPP at 15°C and 35°C (Fig. 5, Table 1).

Discussion

Freshwater mussels occur as large, species-rich aggregations that can account for a significant portion of the benthic biomass in lakes and streams (Vaughn and Hakenkamp 2001). Because they are aggregated, sedentary, and forage in a similar manner (i.e. filter feeders), the potential for species interactions is high. Since they also are ectotherms, temperature should constrain their activity level and thus the magnitude of their contributions to ecosystems. Our results demonstrate that environmental context (temperature) and the functional traits (thermal preference) of numerically dominant species interactively influence resource acquisition and ecosystem services provided by less dominant species, and that this can lead to effects across multiple compartments within ecosystems.

These results also highlight the importance of thermal context to species interactions, with positive effects on the performance of *Megalonaias*, *Obliquaria* and *Amblema* associated with increased *Actinonaias* relative biomass at 25°C and negative effects on all species at 35°C. *Actinonaias* performance also changed relative to its own dominance at 25°C indicating increased intraspecific interactions in addition to interspecific interactions. *Actinonaias* burrows more actively at warm temperatures, presumably seeking thermal refugia

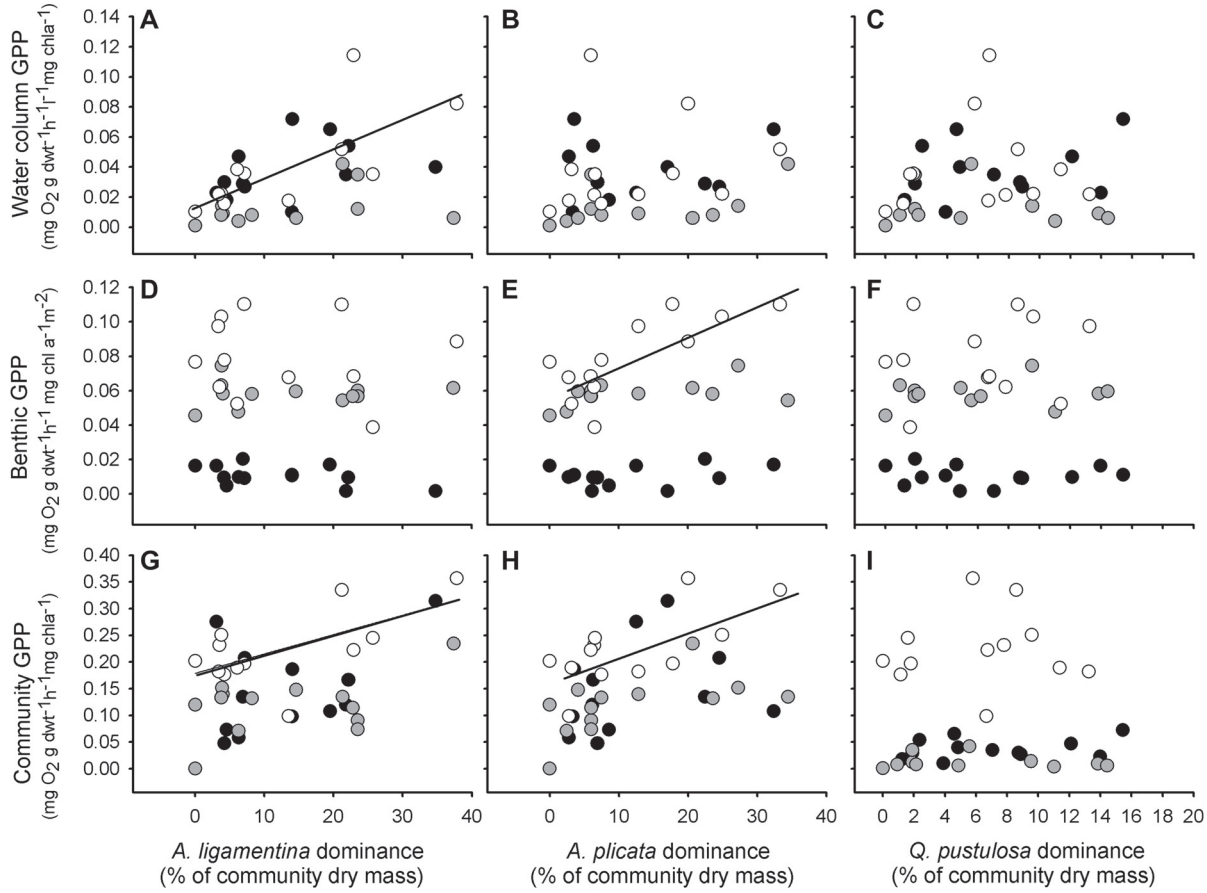

Figure 5. Relationship between water column gross primary production and (A) percent *A. ligamentina* biomass, (B) percent *A. plicata* biomass, (C) percent *Q. pustulosa* biomass. Relationship between benthic gross primary production and (D) percent *A. ligamentina* biomass, (E) percent *A. plicata* biomass, (F) percent *Q. pustulosa* biomass. Relationship between water-column gross primary production and (G) percent *A. ligamentina* biomass, (H) percent *A. plicata* biomass, (I) percent *Q. pustulosa* biomass. Dark circles = 15°C, grey circles and dashed lines = 25°C, and white circles and solid lines = 35°C

(Allen and Vaughn 2009), and this may negatively impact other species by reducing their activity and/or resource assimilation. Although interference competition may explain the negative interactions occurring between species at 35°C, mechanisms for facilitation at 25°C are less apparent.

Shifts in species interactions with changing environments are well documented, particularly in plant communities (Wardle and Peltzer 2003). Most studies have observed facilitation under harsh conditions and competition under more favorable, stable conditions (Stachowicz 2001, Bruno et al. 2003). For example, in legume shrubs Pugnaire and Luque (2001) found positive interactions in water-stressed soil and neutral or negative interactions in fertile, more productive soil. Similar patterns have been observed in intertidal invertebrate–plant communities (Bertness and Leonard 1997) and among intertidal invertebrates (Kawai and Tokeshi 2009). In our study, we observed greater negative interactions at warmer temperatures, but the definition of a 'stressful environment' should differ among mussel species because of their varying thermal optima (Spooner 2007). For example, 35°C may be a stressful environment for *Actinonaias* and *Quadrula*, but a potentially favorable one for other species (*Amblema*, *Megalonaias* and *Obliquaria*) that are more tolerant of warmer environments (Spooner 2007). In a field study comparing mussel body condition across 21 mussel beds in three rivers, we found lower oxygen consumption rates and higher body condition indices in more species-rich mussel beds (Spooner and Vaughn 2009). Mussel condition also was greatest at sites that were more thermally variable, which may imply use of temporal or spatially discrete thermal niches by different mussel species within a bed. However, these patterns may also be explained by greater variation in interactions (facilitation, competition) between species at more environmentally variable sites (Hartley and Jones 2003, Gross 2008).

Species interactions influenced nutrient excretion rates. Ammonia excretion of all species increased at 35°C as a function of *Actinonaias* mesocosm biomass. Additionally, *Quadrula* and *Obliquaria* phosphorus excretion rates increased at 35°C with increasing *Actinonaias* biomass. Others have shown that dominance shifts can result in changes in community-contributed nutrients because of novel species excretion rates (Vanni et al. 2002). For example, McIntyre et al. (2007) found that shifts in cichlid community composition altered the nature of nutrient cycling in African lakes. Although we have predicted similar effects from altering species composition of mussel communities (Vaughn et al. 2008), our results here demonstrate that species interactions can influence the magnitude of individual-based excretion rates of co-occurring species. Further, these effects

have the potential to influence both the quantity and quality of nutrient subsidies and therefore may have lasting stoichiometric implications at higher trophic levels (Hessen et al. 2004, Diehl et al. 2005, McIntyre et al. 2008).

In addition to influencing species interactions, the combined influence of community dominance, species traits and environmental context also translated to divergent effects within experimental mesocosms. Both *Actinonaias* and *Amblema* increased community primary production, yet their relative importance differed between compartments. For example, BGPP increased as a function of *Amblema* biomass at 35°C, yet WCGPP increased as a function *Actinonaias* at 25 and 35°C. The increase in benthic primary production could be explained by differences in benthic algal species composition or novel microbial interactions resulting from *Amblema* activities. Previous laboratory studies have demonstrated that at 35°C *Amblema* filter feeds while *Actinonaias* shifts from aerobic activities to tissue catabolism (Spooner and Vaughn 2008). These subtle differences in thermal traits may also explain greater movement of energy and nutrients from the water column to the sediment in *Amblema* dominated communities, resulting in different benthic algal and/or microbial communities.

WCGPP was strongly related to *Actinonaias* relative biomass, however the mechanism underlying this relationship is less clear and may be from direct or indirect species effects. Although marginally insignificant, both primary production and chlorophyll a in the water column increased at 35°C, yet primary production increased and chlorophyll a decreased at 25°C relative to *Actinonaias* relative biomass. These changes in chlorophyll could result from differential filtration (increased at 25°C and decreased at 35°C), and nutrient excretion related to shifts in *Actinonaias* thermal performance that result in fertilization at 35°C. Water column nutrient concentrations were highest at 35°C, and mostly related to the presence of *Actinonaias.* In addition to directly influencing primary production, *Actinonaias* may also contribute indirectly by influencing the performance of other species (*Amblema*, *Megalonaias*, *Obliquaria, Quadrula*) via competitive (at 35°C) and facilitative (at 25°C) interactions influencing their contributed services (excretion and filtration activities). For example, all species dramatically increased their ammonia excretion rates in the presence of *Actinonaias* dominance, resulting in increased nitrogen and chlorophyll a in the water column at 35°C.

Our results highlight the importance of differential trait expression along environmental gradients, particularly with respect to assumed functional redundancy. The degree to which species traits match the environment has consequences for species interactions and ecosystem processes. For example, at cooler temperatures, ectothermic organisms constrained by temperature should have lower activity levels and for the most part contribute reduced magnitude of services. At warmer temperatures activity levels increase and the relative importance of species shifts according to their thermal traits. For example, at 25°C *Actinonaias* performance positively associates with the local thermal regime resulting in disproportionate effects on ecosystem processes and species interactions relative to other species. However, at 35°C *Actinonaias* traits negatively associate with the local thermal regime, and have disproportionate effects on ecosystem services and species interactions relative to other species.

Understanding how species traits and species interactions map onto a changing environmental landscape is critical to predicting the consequences of shifts in community structure with climate change. Many mussel species in our study region are already experiencing temperatures in the upper end of their thermal tolerance, and we have observed changes in mussel community structure that are linked to stream warming, with thermally tolerant species increasing and thermally sensitive species decreasing in relative abundance (Galbraith et al. 2010). The magnitude, periodicity and duration of droughts are increasing in the southern US, and mean summer temperatures are predicted to increase by as much as 4°C over the next 50 years (Mulholland et al. 1997, IPCC 2001). These projected temperature increases, and associated decreased precipitation, will likely profoundly influence mussel community structure and the services that they provide to ecosystems.

Most studies investigating the ecosystem services provided by communities have focused on the role of species richness by comparing the relative yield of species monocultures to those of multiple species (polycultures) (Petchey 2003). The underlying premise of this approach assumes that the resulting effects of species richness are due to either: 1) interspecific competition/facilitation resulting in enhanced ecosystem services (productivity, stability) (Loreau et al. 2001); or 2) the inclusion of species with novel traits that are better adapted to the experimental conditions, resulting in overall greater ecosystem effects (productivity, stability, etc.) (Loreau and Hector 2001). This approach is widely accepted and has demonstrated singular or combined effects of species richness and species identity on ecosystem services (Cardinale et al. 2002, Fox 2005). Our study, which held species richness constant and manipulated the relative dominance of species, allowed us to demonstrate that species traits, species dominance and environmental context interactively contribute to the ecosystem services provided by communities and important ecological processes within ecosystems. Our results suggest that the direction and magnitude of species interactions are related to both community composition and environmental context, and suggest that caution should be used in interpreting the results of biodiversity experiments that simply manipulate the number of species.

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Appendix

Table A1. Experimental design illustrating the manipulation (number of individuals) of species dominance within each stream. Stream assignment was randomly selected for each experimental run (temperature).

Stream	*A. ligamentina*	*A. plicata*	*Q. pustulosa*	*M. nervosa*	*O. reflexa*
1	4	1	7	3	2
2	7	2	1	3	4
3	1	4	7	3	2
4	2	7	4	2	2
5	2	4	1	7	3
6	0	0	0	0	0
7	7	2	4	3	1
8	2	1	7	4	3
9	4	1	2	3	7
10	7	4	2	1	3
11	1	2	4	3	7
12	2	7	1	3	4
13	0	0	0	0	0
14	4	7	2	1	3

Table A2. Pearson correlation coefficients for species biomass demonstrating that dominance treatment assignments were independent of each other (r-value, p-value in parenthesis).

	A. ligamentina	*A. plicata*	*Q. pustulosa*	*M. nervosa*	*O. reflexa*
A. ligamentina	1	0.08 (0.77)	0.01 (0.97)	0.08 (0.79)	0.16 (0.58)
A. plicata		1	0.04 (0.90)	0.10 (0.73	0.11 (0.70)
Q. pustulosa			1	0.29 (0.32)	0.04 (0.88)
M. nervosa				1	0.38 (0.19)
O. reflexa					1

Table A3. Results of generalized linear model explaining the effects of temperature and species dominance manipulations on mussel performance. Slope parameter estmates in parentheses. Significant p-values in bold.

			Actinonaias ligamentina						
Response	Predictor	Paramater	Full model	Temp	Species	Temp× Species	15×Species	25×Species	35×Species
Oxygen consumption	*Actinonaias*	$X^2_{(DF)}$	AIC = 95.2	$0.9_{(2)}$	$12.6_{(1)}$	$7.9_{(2)}$	$1.6_{(1)}$ B=0.022	$25.7_{(1)}$ B=0.078	$3.8_{(1)}$ B=0.031
		p-value		0.6	**0**	**0.02**	0.7	**<0.001**	0.054
	Amblema	$X^2_{(DF)}$	AIC = 111.1	$1.9_{(2)}$	$1.0_{(1)}$	$0.4_{(2)}$	$0.07_{(1)}$ B=0.006	$2.9_{(1)}$ (B=0.035)	$0.06_{(1)}$ B=0.005
		p-value		0.396	0.3	0.8	0.8	0.1	0.811
	Quadrula	$X^2_{(DF)}$	AIC = 111.9	$1.9_{(2)}$	$0.3_{(1)}$	$0.2_{(2)}$	$1.1_{(1)}$ B=-0.047	$0.09_{(1)}$ B=0.014	$0.5_{(1)}$ B=-0.033
		p-value		0.38	0.6	0.92	0.3	0.8	0.5
Condition	*Actinonaias*	$X^2_{(DF)}$	AIC = 134.7	$1.72_{(2)}$	$0.2_{(1)}$	$6.5_{(2)}$	$1.5_{(1)}$ B=0.038	$3.1_{(1)}$ B=0.048	$14.5_{(1)}$ B=-0.106
		p-value		0.422	0.7	**0.038**	0.2	0.08	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 138.3	$15.979_{(2)}$	$1.0_{(1)}$	$1.7_{(2)}$	$0.006_{(1)}$ B=0.004	$0.2_{(1)}$ B=0.015	$5.3_{(1)}$ B=-0.089
		p-value		**<0.001**	0.3	0.4	0.9	0.7	**0.02**
	Quadrula	$X^2_{(DF)}$	AIC = 138.9	$11.873_{(2)}$	$0.4_{(1)}$	$1.4_{(2)}$	$0.1_{(1)}$ B=0.019	$0.02_{(1)}$ B=0.009	$6.7_{(1)}$ B=-0.195
		p-value		**0.003**	0.5	0.5	0.8	0.9	**0.01**
Ammonia excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 108.4	$2.488_{(2)}$	$11.7_{(1)}$	$18.7_{(2)}$	$2.1_{(1)}$ B=0.031	$0.01_{(1)}$ B=-0.002	$43.3_{(1)}$ B=0.128
		p-value		0.288	**0.001**	**<0.001**	0.1	0.9	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 130.7	$3.0_{(2)}$	$0.2_{(1)}$	$0.8_{(2)}$	$0.01_{(1)}$ B=-0.003	$1.5_{(1)}$ B=-0.034	$3.3_{(1)}$ B=0.069
		p-value		**0.01**	0.2	0.1	0.9	0.2	0.1
	Quadrula	$X^2_{(DF)}$	AIC = 131.2	$5.5_{(2)}$	$0.2_{(1)}$	$0.3_{(2)}$	$0.1_{(1)}$ B=-0.018	$1.9_{(1)}$ B=-0.090	$1.7_{(1)}$ B=0.081
		p-value		0.063	0.6	0.8	0.8	0.1	0.2
Phosphorus excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −174.1	$21.4_{(2)}$	$1.1_{(1)}$	$1.9_{(2)}$	$8.8_{(1)}$ B=-0.001	$0.4_{(1)}$ B=0.00	$0.01_{(1)}$ B=0.000
		p-value		**<0.001**	0.3	0.4	**0.003**	0.5	0.9
	Amblema	$X^2_{(DF)}$	AIC = −172.1	$13.9_{(2)}$	$0.2_{(1)}$	$0.1_{(2)}$	$7.9_{(1)}$ B=-0.001	$2.5_{(1)}$ B=0.001	$0.1_{(1)}$ B=0.000
		p-value		**0.001**	0.7	1	**0.005**	0.1	0.7
	Quadrula	$X^2_{(DF)}$	AIC = −164.5	$13.9_{(2)}$	$0.02_{(1)}$	$1.2_{(2)}$	$7.0_{(1)}$ B=-0.003	$1.8_{(1)}$ B=0.001	$0.7_{(1)}$ B=0.001
		p-value		**0.001**	0.9	0.5	**0.008**	0.2	0.4
N:P excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −154.1	$31.2_{(2)}$	$10.4_{(1)}$	$11.5_{(2)}$	$14.8_{(1)}$ B=2.092	$0.1_{(1)}$ B=-0.439	$8.9_{(1)}$ B=1.500
		p-value		**<0.001**	**0.001**	**0.003**	**<0.001**	0.4	**0.003**
	Amblema	$X^2_{(DF)}$	AIC = −162.1	$19.82_{(2)}$	$0.3_{(1)}$	$2.1_{(2)}$	$4.7_{(1)}$ B=1.378	$3.3_{(1)}$ B=-1.071	$0.69_{(1)}$ B=0.498
		p-value		**<0.001**	0.6	0.3	**0.03**	0.07	0.4
	Quadrula	$X^2_{(DF)}$	AIC = −162.2	$10.101_{(2)}$	$0.4_{(1)}$	$0.8_{(2)}$	$4.8_{(1)}$ B=2.545	$6.8_{(1)}$ B=-3.168	$0.3_{(1)}$ B=-0.625
		p-value		**0.006**	0.5	0.7	**0.03**	**0.009**	0.6

(Continued)

Table A3. (*Continued*).

			Amblema plicata						
Response	Predictor	Paramater	Full model	Temp	Species	Temp×Species	15×Species	25×Species	35×Species
Oxygen consumption	*Actinonaias*	$X^2_{(DF)}$	AIC = 127.1	$1.2_{(2)}$	$0_{(1)}$	$0.2_{(2)}$	$0.2_{(1)}$ B=−0.013	$0_{(1)}$ B=0	$0.2_{(1)}$ B=0.010
		p-value		0.5	1	0.9	0.6	1	0.7
	Amblema	$X^2_{(DF)}$	AIC = 121.9	$0.2_{(2)}$	$3.5_{(1)}$	$2.2_{(2)}$	$0.07_{(1)}$ B=0.007	$2.2_{(1)}$ B=0.035	$3.3_{(1)}$ B=0.064
		p-value		0.9	0.06	0.3	0.8	0.1	0.1
	Quadrula	$X^2_{(DF)}$	AIC = 124.8	$0.2_{(1)}$	$2.1_{(1)}$	$0.6_{(1)}$	$0.3_{(1)}$ B=0.029	$0.9_{(1)}$ B=0.052	$3.9_{(1)}$ B=0.107
		p-value		0.9	0.1	0.7	0.6	0.3	0.06
Condition	*Actinonaias*	$X^2_{(DF)}$	AIC = 132.0	13.0(2)	$7.9_{(1)}$	$4.2_{(2)}$	$28.1_{(1)}$ B=−0.176	$1.8_{(1)}$ B=0.040	$3.2_{(1)}$ B=-0.055
		p-value		**0.002**	**0.005**	**0.012**	**<0.001**	0.2	**0.04**
	Amblema	$X^2_{(DF)}$	AIC = 142.0	$17.6_{(2)}$	$0.2_{(1)}$	$0.05_{(2)}$	$5.5_{(1)}$ B=−0.096	$5.6_{(1)}$ B=0.090	$0.5_{(1)}$ B=0.029
		p-value		**<0.001**	0.7	1	**0.019**	**0.02**	0.5
	Quadrula	$X^2_{(DF)}$	AIC = 139.8	23.9(1)	0.6(1)	$1.8_{(1)}$	$3.1_{(1)}$ B=−0.145	$4.9_{(1)}$ B=0.192	$0.9_{(1)}$ B=0.080
		p-value		**<0.001**	0.4	0.4	0.08	**0.03**	0.4
Ammonia excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 141.1	$0.8_{(2)}$	$3.3_{(1)}$	$13.3_{(2)}$	$0.000_{(1)}$ B=0.002	$0.1_{(1)}$ B=−0.01	$21.6_{(1)}$ B=0.140
		p-value		0.8	0.07	**0.001**	1	0.7	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 155.3	$2.5_{(2)}$	$0.001_{(1)}$	$0.05_{(2)}$	$0.3_{(1)}$ B=−0.025	$1.0_{(1)}$ B=−0.038	$12.1_{(1)}$ B=0.061
		p-value		0.3	0.9	0.9	0.6	0.3	0.1
	Quadrula	$X^2_{(DF)}$	AIC = 152.5	$0.7_{(1)}$	$2.7_{(1)}$	$0.5_{(1)}$	$0.6_{(1)}$ B=0.058	$0.1_{(1)}$ B=0.029	$0.3_{(1)}$ B=0.244
		p-value		0.7	0.1	0.8	0.5	0.7	0.3
Phosphorus excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −167.3	$11.9_{(2)}$	$0.1_{(1)}$	$0.09_{(2)}$	$9.8_{(1)}$ B=−0.002	$1.8_{(1)}$ B=0.001	$0.6_{(1)}$ B=0.000
		p-value		**0.002**	0.7	1	**0.002**	0.2	0.4
	Amblema	$X^2_{(DF)}$	AIC = −168.1	$18.4_{(2)}$	$0.01_{(1)}$	$0.9_{(2)}$	$5.3_{(1)}$ B=−0.001	$1.7_{(1)}$ B=0.001	$1.9_{(1)}$ B=0.001
		p-value		**<0.001**	0.8	0.6	**0.02**	0.2	0.2
	Quadrula	$X^2_{(DF)}$	AIC = −179.9	$34.1_{(1)}$	$6.1_{(1)}$	$8.6_{(1)}$	$13.6_{(1)}$ B=−0.004	$0.5_{(1)}$ B=−0.001	$0.001_{(1)}$ B=0.000
		p-value		**<0.001**	**0.01**	**0.013**	**<0.001**	0.5	1
N:P excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 377.1	$8.4_{(2)}$	$0.2_{(1)}$	$4.5_{(2)}$	$2.4_{(1)}$ B=1.462	$1.2_{(1)}$ B=−0.925	$0.9_{(1)}$ B=0.831
		p-value		**0.015**	0.6	0.1	0.1	0.3	0.3
	Amblema	$X^2_{(DF)}$	AIC = 379.1	9.6(2)	$0.7_{(1)}$	$2.2_{(2)}$	$0.2_{(1)}$ B=0.396	$2.2_{(1)}$ B=−1.393	$0.2_{(1)}$(B=-0.472
		p-value		**0.008**	0.4	0.3	0.7	0.1	0.6
	Quadrula	$X^2_{(DF)}$	AIC = 371.3	$2.2_{(1)}$	$11.3_{(1)}$	0.5(1)	$20.6_{(1)}$ B=7.496	$1.2_{(1)}$ B=1.911	$2.3_{(1)}$ B=3.919
		p-value		0.335	**0.001**	0.8	**<0.001**	0.3	0.1

			Megalonaias nervosa						
Response	Predictor	Paramater	Full model	Temp	Species	Temp×Species	15×Species	25×Species	35×Species
Oxygen consumption	*Actinonaias*	$X^2_{(DF)}$	AIC = 37.5	$1.2_{(2)}$	$0.3_{(1)}$	$17.2_{(2)}$	$0.2_{(1)}$ B=−0.004	$6.4_{(1)}$ (B=−0.018)	$17.6_{(1)}$ B=0.003
		p-value		0.6	0.5	**<0.001**	0.6	**0.012**	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 50.4	$2.6_{(2)}$	$0.0_{(1)}$	$1.4_{(2)}$	$0.5_{(1)}$ B=−0.007	$3.2_{(1)}$ (B=−0.016)	$3.1_{(1)}$ B=0.022
		p-value		0.3	1	0.5	0.5	0.07	0.07
	Quadrula	$X^2_{(DF)}$	AIC = 46.8	$16.3_{(2)}$	$0.6_{(1)}$	$5.1_{(2)}$	$0.6_{(1)}$ B=−0.017	$0.7_{(1)}$ (B=−0.019)	$1.1_{(1)}$ B=0.024
		p-value		**<0.001**	0.4	0.08	0.4	0.4	0.3
Condition	*Actinonaias*	$X^2_{(DF)}$	AIC = 146.9	$1.0_{(2)}$	$1.3_{(1)}$	$4.0_{(2)}$	$0.1_{(1)}$ B=0.012	$13.1_{(1)}$ (B=0.115)	$1.6_{(1)}$ B=−0.042
		p-value		0.6	0.2	0.1	0.7	**<0.001**	0.2
	Amblema	$X^2_{(DF)}$	AIC = 148.2	$3.0_{(2)}$	$0.03_{(1)}$	$4.0_{(2)}$	$1.4_{(1)}$ B=−0.046	$6.6_{(1)}$ (B=0.091)	$2.5_{(1)}$ B=−0.061
		p-value		0.2	0.9	0.1	0.2	**0.01**	0.1
	Quadrula	$X^2_{(DF)}$	AIC = 150.8	$6.8_{(2)}$	$0.04_{(1)}$	$1.2_{(2)}$	$0.1_{(1)}$ B=−0.031	$1.7_{(1)}$ (B=0.110)	$2.9_{(1)}$ B=−0.144
		p-value		**0.033**	0.8	0.6	0.7	0.2	0.09
Ammonia excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 89.9	$2.7_{(2)}$	$1.9_{(1)}$	$18.1_{(2)}$	$0.008_{(1)}$ B=0.001	$1.2_{(1)}$ (B=−0.016)	$19.1_{(1)}$ B=0.066
		p-value		0.2	0.2	**<0.001**	0.9	0.3	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 101.5	$2.7_{(2)}$	$0.4_{(1)}$	$4.8_{(2)}$	$0.2_{(1)}$ B=−0.009	$0.5_{(1)}$ (B=−0.014)	$0.7_{(1)}$ B=0.051
		p-value		0.3	0.5	0.09	0.7	0.5	0.7
	Quadrula	$X^2_{(DF)}$	AIC = 106.0	$2.5_{(2)}$	$0.3_{(1)}$	$0.05_{(2)}$	$0.1_{(1)}$ B=0.014	$0.2_{(1)}$ (B=−0.021)	$3.3_{(1)}$ B=0.078
		p-value		0.3	0.6	1	0.7	0.6	0.07
Phosphorus excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −206.4	$12.9_{(2)}$	$0.6_{(1)}$	$0.1_{(2)}$	$8.0_{(1)}$ B=−0.001	$2.2_{(1)}$ (B=0)	$0.1_{(1)}$ B=0
		p-value		**<0.001**	0.4	1	**0.005**	0.1	0.7
	Amblema	$X^2_{(DF)}$	AIC = −207.9	$15.8_{(2)}$	$1.5_{(1)}$	$0.6_{(2)}$	$9.5_{(1)}$ B=−0.001	$1.2_{(1)}$ (B=0)	$0.2_{(1)}$ B=0
		p-value		**<0.001**	0.2	0.7	**0.002**	0.3	0.7
	Quadrula	$X^2_{(DF)}$	AIC = −207.9	$17.5_{(2)}$	$0.9_{(1)}$	$1.4_{(2)}$	$7.0_{(1)}$ B=−0.002	$1.1_{(1)}$ (B=0.001)	$0.2_{(1)}$ B=0
		p-value		**<0.001**	0.4	0.5	**0.008**	0.3	0.7
N:P excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 310.2	$36.6_{(2)}$	$2.0_{(1)}$	$1.4_{(2)}$	$5.4_{(1)}$ B=1.263	$3.4_{(1)}$ (B=−0.896)	$4.7_{(1)}$ B=1.144
		p-value		**<0.001**	0.2	0.5	**0.02**	0.07	**0.03**
	Amblema	$X^2_{(DF)}$	AIC = 299.5	$80.6_{(2)}$	$4.0_{(1)}$	$13.4_{(2)}$	$1.6_{(1)}$ B=0.772	$2.2_{(1)}$ (B=−0.846)	$1.9_{(1)}$ B=−1.358
		p-value		**<0.001**	**0.04**	**0.001**	0.2	0.1	0.08
	Quadrula	$X^2_{(DF)}$	AIC = 312.2	$18.8_{(2)}$	$0.6_{(1)}$	$0.3_{(2)}$	$15.0_{(1)}$ B=3.83	$0.7_{(1)}$ (B=−0.861)	$3.6_{(1)}$ B=−1.928
		p-value		**<0.001**	0.06	0.7	**<0.001**	0.4	0.06

(Continued)

Table A3. (*Continued*).

			Obliquaria reflexa						
Response	Predictor	Paramater	Full model	Temp	Species	Temp× Species	15×Species	25×Species	35×Species
Oxygen consumption	*Actinonaias*	$X^2_{(DF)}$	AIC = 124.1	$6.2_{(2)}$	$1.7_{(1)}$	$15.8_{(2)}$	$1.8_{(1)}$ B=−0.037	6.0(1) B=−0.024	$23.9_{(1)}$ B=0.124
		p-value		**0.05**	0.2	**<0.001**	0.2	**0.02**	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 138.1	$7.2_{(2)}$	$0.001_{(1)}$	$0.4_{(2)}$	$3.1_{(1)}$ B=−0.062	$0.6_{(1)}$ B=−0.026	$3.6_{(1)}$ B=0.082
		p-value		**0.027**	1	0.8	0.1	0.4	0.09
	Quadrula	$X^2_{(DF)}$	AIC = 132.7	$14.7_{(2)}$	$0.2_{(1)}$	$6.2_{(2)}$	$4.2_{(1)}$ B=−0.141	$0.01_{(1)}$ B=0.007	$3.4_{(1)}$ B=0.131
		p-value		**0.001**	0.6	**0.04**	**0.04**	0.9	0.07
Condition	*Actinonaias*	$X^2_{(DF)}$	AIC = 57.3	$22.4_{(2)}$	$0.5_{(1)}$	$6.2_{(2)}$	$0.06_{(1)}$ B=−0.003	$0.1_{(1)}$ B=−0.004	$11.8_{(1)}$ B=−0.016
		p-value		**<0.001**	0.5	**0.05**	0.8	0.8	**0.001**
	Amblema	$X^2_{(DF)}$	AIC = 60.0	$6.2_{(2)}$	$2.6_{(1)}$	$0.6_{(2)}$	$0.04_{(1)}$ B=−0.002	$0.04_{(1)}$ B=0.002	$11.3_{(1)}$ B=0.039
		p-value		**0.045**	0.1	0.7	0.85	0.9	0.09
	Quadrula	$X^2_{(DF)}$	AIC = 62.1	$3.2_{(2)}$	$0.7_{(1)}$	$0.4_{(2)}$	$2.2_{(1)}$ B=−0.038	$2.5_{(1)}$ B=−0.037	$3.2_{(1)}$ B=0.042
		p-value		0.2	0.4	0.8	0.09	0.1	0.08
Ammonia excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 201.7	$4.9_{(2)}$	$8.5_{(1)}$	$15.6_{(2)}$	$3.8_{(1)}$ B=0.154	$0.06_{(1)}$ B=0.017	$19.8_{(1)}$ B=0.326
		p-value		0.09	**0.003**	**<0.001**	0.05	0.8	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 220.4	$0.9_{(2)}$	$0.01_{(1)}$	$0.5_{(2)}$	$0.03_{(1)}$ B=0.016	$0.8_{(1)}$ B=−0.082	$0.9_{(1)}$ B=0.097
		p-value		0.6	0.9	0.8	0.9	0.4	0.3
	Quadrula	$X^2_{(DF)}$	AIC = 220.5	$1.5_{(2)}$	$0.001_{(1)}$	$0.4_{(2)}$	$0.0_{(1)}$ B=0.012	$0.5_{(1)}$ B=−0.154	$0.5_{(1)}$ B=0.149
		p-value		0.5	1	0.8	1	0.5	0.5
Phosphorus excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −76.6	$5.9_{(2)}$	$0.5_{(1)}$	$1.0_{(2)}$	$1.4_{(1)}$ B=−0.002	$5.4_{(1)}$ B=0.004	$0.2_{(1)}$ B=0.001
		p-value		**0.05**	0.5	0.6	0.2	**0.02**	0.6
	Amblema	$X^2_{(DF)}$	AIC = −78.8	2.1(2)	$2.2_{(1)}$	$1.7_{(2)}$	$0.7_{(1)}$ B=−0.001	$13.0_{(1)}$ B=0.005	$0.3_{(1)}$ B=0.001
		p-value		0.3	0.1	0.4	0.4	**<0.001**	0.6
	Quadrula	$X^2_{(DF)}$	AIC = −78.5	$12.0_{(2)}$	$1.4_{(1)}$	$2.1_{(2)}$	$4.1_{(1)}$ B=−0.007	$0.1_{(1)}$ B=0.001	$1.4_{(1)}$ B=−0.004
		p-value		**0.003**	0.2	0.3	**0.04**	0.7	0.2
N:P excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 318.4	$1.9_{(2)}$	$4.4_{(1)}$	$13.1_{(2)}$	$0.4_{(1)}$ B=−0.233	$0.1_{(1)}$ B=0.122	$25.0_{(1)}$ B=1.786
		p-value		0.4	**0.04**	**0.001**	0.5	0.7	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 333.1	$5.8_{(2)}$	$0.02_{(1)}$	$0.1_{(2)}$	$1.7_{(1)}$ B=−0.671	$0.1_{(1)}$ B=−0.182	$1.8_{(1)}$ B=0.689
		p-value		0.06	0.9	0.9	0.2	0.7	0.2
	Quadrula	$X^2_{(DF)}$	AIC = 330.7	$1.2_{(2)}$	$1.7_{(1)}$	$1.1_{(2)}$	$0.4_{(1)}$ B=−0.552	$0.9_{(1)}$ B=0.918	$0.1_{(1)}$ B=0.013
		p-value		**0.003**	0.5	0.9	**0.001**	0.1	0.4

			Quadrula pustulosa						
Response	Predictor	Paramater	Full model	Temp	Species	Temp× Species	15×Species	25×Species	35×Species
Oxygen consumption	*Actinonaias*	$X^2_{(DF)}$	AIC = 194.0	$14.3_{(2)}$	$0.1_{(1)}$	$2.2_{(2)}$	$4.2_{(1)}$ B=−0.164	$2.3_{(1)}$ B=−0.108	$6.5_{(1)}$ B=0.186
		p-value		**0.001**	0.8	0.3	**0.04**	0.1	**0.011**
	Amblema	$X^2_{(DF)}$	AIC = 198.3	12.9(2)	$0.1_{(1)}$	$3.8_{(2)}$	$2.9_{(1)}$ B=−0.136	$1.6_{(1)}$ B=−0.092	$5.5_{(1)}$ B=0.264
		p-value		**0.002**	0.8	0.1	0.085	0.2	0.1
	Quadrula	$X^2_{(DF)}$	AIC = 197.7	3.8(2)	0.004(1)	$3.1_{(2)}$	$5.6_{(1)}$ B=−0.333	$1.1_{(1)}$ B=−0.157	$6.9_{(1)}$ B=0.531
		p-value		0.2	1	0.2	**0.019**	0.3	0.08
Condition	*Actinonaias*	$X^2_{(DF)}$	AIC = 38.8	$7.7_{(2)}$	$2.5_{(1)}$	$0.3_{(2)}$	$6.0_{(1)}$ B=−0.021	$1.6_{(1)}$ B=0.01	$5.0_{(1)}$ B=−0.017
		p-value		**0.02**	0.1	0.9	**0.015**	0.2	**0.03**
	Amblema	$X^2_{(DF)}$	AIC = 34.5	$21.5_{(2)}$	$_{1.0(1)}$	$7.1_{(2)}$	$0.002_{(1)}$ B=0	$5.4_{(1)}$ B=0.021	$0.5_{(1)}$ B=−0.007
		p-value		**<0.001**	0.3	**0.029**	1	**0.02**	0.5
	Quadrula	$X^2_{(DF)}$	AIC = 40.4	$4.5_{(2)}$	$0.3_{(1)}$	$0.9_{(2)}$	$5.1_{(1)}$ B=−0.039	$3.6_{(1)}$ B=0.034	$1.6_{(1)}$ B=−0.023
		p-value		0.1	0.6	0.6	**0.024**	0.06	0.2
Ammonia excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 199.0	$0.5_{(2)}$	$4.0_{(1)}$	$5.0_{(2)}$	$1.4_{(1)}$ B=0.086	$0.02_{(1)}$ B=0.009	$11.2_{(1)}$ B=0.223
		p-value		0.8	**0.047**	0.09	0.2	0.9	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 205.3	$2.2_{(2)}$	$0.3_{(1)}$	$1.8_{(2)}$	$0.7_{(1)}$ B=0.071	$0.6_{(1)}$ B=−0.059	$0.9_{(1)}$ B=0.079
		p-value		0.3	0.6	0.4	0.4	0.4	0.3
	Quadrula	$X^2_{(DF)}$	AIC = 205.2	$0.8_{(2)}$	$1.0_{(1)}$	$1.4_{(2)}$	$0.2_{(1)}$ B=0.073	$0.002_{(1)}$ B=−0.007	$3.5_{(1)}$ B=0.313
		p-value		0.7	0.3	0.5	0.7	1	0.06
Phosphorus excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = −105.7	$4.7_{(2)}$	$3.8_{(1)}$	$5.4_{(2)}$	$2.6_{(1)}$ B=−0.002	$30.3_{(1)}$ B=0.005	$0.2_{(1)}$ B=0
		p-value		0.09	**0.05**	0.07	0.1	**<0.001**	0.7
	Amblema	$X^2_{(DF)}$	AIC = −98.2	$18.7_{(2)}$	$0.7_{(1)}$	$0.6_{(2)}$	$4.9_{(1)}$ B=−0.003	$3.3_{(1)}$ B=0.002	$1.4_{(1)}$ B=−0.002
		p-value		**<0.001**	0.4	0.7	**0.027**	0.07	0.2
	Quadrula	$X^2_{(DF)}$	AIC = −102.9	$27.3_{(2)}$	$2.1_{(1)}$	$4.2_{(2)}$	$7.5_{(1)}$ B=−0.008	$0.7_{(1)}$ B=0.003	$1.6_{(1)}$ B=−0.004
		p-value		**<0.001**	0.1	0.1	**0.006**	0.4	0.2
N:P excretion	*Actinonaias*	$X^2_{(DF)}$	AIC = 349.59	$0.4_{(2)}$	$3.1_{(1)}$	$9.0_{(2)}$	$0.2_{(1)}$ B=−0.280	$0_{(1)}$ B=-0.003	$20.4_{(1)}$ B=2.441
		p-value		0.8	0.08	**0.011**	0.6	1	**<0.001**
	Amblema	$X^2_{(DF)}$	AIC = 360.0	$3.4_{(2)}$	$0.003_{(1)}$	$0.5_{(2)}$	$1.2_{(1)}$ B=−0.806	$0.8_{(1)}$ B=−0.596	$2.7_{(1)}$ B=1.277
		p-value		0.2	1	0.8	0.3	0.4	0.08
	Quadrula	$X^2_{(DF)}$	AIC = 358.9	$1.4_{(2)}$	$1.1_{(1)}$	$0.6_{(2)}$	$0.2_{(1)}$ B=−0.566	$0.2_{(1)}$ B=0.622	$0.9_{(1)}$ B=0.968
		p-value		0.5	0.3	0.7	0.7	0.7	0.2