Species richness and temperature influence mussel biomass: a partitioning approach applied to natural communities

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Abstract. To increase the generality of biodiversity–ecosystem function theory, studies must be expanded to include real communities in a variety of systems. We modified J. W. Fox's approach to partition the influence of species richness on standing crop biomass (net biodiversity effect) of 21 freshwater mussel communities into trait-independent complementarity, trait-dependent complementarity (species with particular traits dominate without impacting other species), and dominance effects (species with particular traits dominate at the expense of others). Overall, species-rich mussel communities have greater biomass than predicted based on average biomass across the region. This effect is largely due to trait-independent complementarity with less abundant species having higher body condition and reduced metabolic rates in species-rich communities. These measures are positively correlated with spatial and temporal thermal variation, suggesting that use of thermal niches as habitat may be important to species coexistence and performance, and emphasizing that knowledge of species traits and environmental context are important to understanding biodiversity–ecosystem function dynamics.

Key words: biodiversity; dominance; ecosystem function; regional vs. local; species traits; thermal niche; trait-dependent complementarity; trait-independent complementarity; Unionidae.

Introduction

Studies investigating the functional role of communities in response to species decline and anticipated shifts in environmental regime have evolved from documenting relationships between natural patterns of species richness and attributes of ecosystem function (Mittelbach et al. 2001) to experimental manipulations of species or functional group richness in controlled and semi-natural systems (Petchey and Gaston 2002, Schmid and Hector 2004). While early studies were performed in terrestrial annual plant communities, newer work has expanded to marine and freshwater ecosystems encompassing both horizontal and vertical levels of biodiversity (Downing 2005, Bruno et al. 2006, Duffy et al. 2007). Although biodiversity–ecosystem function research topics have ranged from community invasibility (Turnbull et al. 2005) to ecosystem resilience to disturbance (Pfisterer and Schmidt 2002), most studies have focused on biomass accrual of primary producers and consumers (Duffy 2002, Wardle and Peltzer 2003). The interpretation and analysis of these experiments have progressed from comparisons of biomass across treatments to examining changes in relative performance (yield) among component species within and between treatments (Loreau and Hector 2001, Fox 2005).

Species interactions that lead to biodiversity effects may be due to the relative contribution of the whole community (complementarity among species), the separate effects of dominant species (selection effect), or both factors. Complementarity occurs (1) via facilitative interactions enhancing the efficiency of resource processing and assimilation or (2) from resource partitioning which increases overall resource use (Hooper 1998, Mulder et al. 2001, Cardinale et al. 2002). The selection effect occurs when dominant species outperform others in polyculture resulting in greater ecosystem effects in species-rich treatments (Loreau 1998, Wardle 1999). The selection or sampling effect, as it pertains to biodiversity experiments, occurs as a result of including a species in mixture that has strong monoculture performance. The probability of including such a species increases with species richness and can lead to inflated biodiversity effects in-high richness treatments (Huston 1997). On the other hand, species may become dominant in treatments because their traits are favored under particular environmental conditions (Loreau and Hector 2001, Fox 2005), and thus either contribute more to ecosystem function, outcompete other species, or both.

The lack of detailed information about trait expression and species interactions within most biodiversity experiments makes it difficult to distinguish complementarity from the selection effect. Loreau and Hector (2001) used a modification of Price's (Price 1970) selection equation to demonstrate that the selection component (i.e., dominant species effect) of the net biodiversity effect was analogous to natural selection of

traits associated with high-yield monoculture species, thus favoring their dominance over others in polyculture (Sala 2001). Fox (2005) expanded this approach by partitioning biodiversity effects into three distinct components: (1) Trait-independent complementarity (TI complementarity), where the yield of species in polyculture increases independently of their traits, and without negatively impacting co-occurring species (equivalent to complementarity as defined by Loreau and Hector [2001]); (2) the dominance effect, a true analogue of natural selection in which species with particular traits dominate at the expense of other species; and (3) trait-dependent complementarity (TD complementarity), where a species' polyculture yield increases due to the expression of their traits, but not at the expense of other species.

The additive partition technique primarily has been applied to manipulative experiments, where yields from monocultures and mixtures can be explicitly compared (Petchey 2003), but where experimental assemblages may not represent naturally co-occurring species. Natural communities are the net result of multiple interactive processes (intra- and interspecific interactions, biogeographical constraints, recruitment limitations), each of which are relevant to understanding species occurrences, dominance, and subsequent contributions to ecosystem function (Brown 1984, Palmer et al. 1996, Stachowicz 2001). In contrast, environmental conditions in manipulative experiments are often restricted and may favor the specific traits of a few species, leading to their dominance. To increase our understanding of services provided by real communities to ecosystem function, studies must expand beyond experimental plots to natural communities (Srivastava and Vellend 2005).

Freshwater mussel (Bivalvia: Unionoida) communities are an excellent system to examine questions of biodiversity and ecosystem function because they represent very different life history and habitat characteristics from most organisms studied to date, expanding the generality of existing theories. Mussels are long-lived, burrowing, sessile, filter feeders that provide important ecological services, coupling energy from the water column to the benthos through filtration, biodeposition of feces and pseudofeces, and nutrient mineralization (Vaughn and Hakenkamp 2001, Spooner and Vaughn 2006). Mussels often occur as aggregated, multispecies assemblages (beds) in lakes and streams. Mussel beds can range in area from <50 to >5000 m^2 and mussel densities within beds are typically 10 to 100 times higher than streambed areas outside of beds (Strayer et al. 2004, Vaughn and Spooner 2006). The species diversity and biomass of such beds can be substantial; for example, beds we have observed in the south-central United States can contain up to 30 species with an overall biomass of 25 kg/m^2 (wet mass including shell). Despite occurring as these speciose assemblages, very few differences in traditional physical habitat or

dietary niches have been documented (Vaughn and Hakenkamp 2001, Strayer et al. 2004). However, recent laboratory studies found that the physiological performance of mussel species (i.e., respiration, filtration, excretion) varies along temperature gradients, thus temperature may be used by mussels to partition spatial and temporal resources (Baker and Hornbach 2001, Spooner 2007, Vaughn et al. 2008).

Here we expand biodiversity–ecosystem function theory using species-specific biomass data of natural mussel communities to test predictions relating to species performance and biodiversity effects among 21 mussel beds. Using the criteria outlined by Fox (2005), measures of mussel physiological condition (Fulton's K and mass-specific respiration), and estimates of site-specific niche breadth (spatial and temporal thermal variation), we tested the following predictions:

1) If all species within a community benefit via TI complementarity then the condition of both numerically dominant (major) and subordinate (minor) species within communities should correlate positively to the magnitude of TI complementarity. Conversely, if the dominance effect is the result of selecting traits associated with major species at the expense of minor species, the magnitude of the dominance effect will correlate positively with major species condition and negatively with minor species condition. Likewise, if TD complementarity is the result of selecting traits associated with major species without influencing minor species, there should be a positive relationship between the magnitude of the dominance effect and major species body condition, and no relationship with minor species body condition.

2) If TI complementarity leads to increased community biomass through niche differentiation, its magnitude should correlate positively with the number of thermal niches (spatial and temporal thermal variance) at a given site. Alternatively, if TD complementarity and dominance species effects result from preferential selection and expression of traits associated with dominant species, then the magnitude of both factors should be highest at sites exhibiting temperatures closest to the thermal optima of dominant species and, therefore, would be independent of the number of thermal niches.

METHODS

Study area and sampling methods

Our study was conducted in the Ouachita Highlands of eastern Oklahoma and western Arkansas, an area of mid-sized, minimally disturbed streams (Mayden 1985) with a largely intact mussel fauna. In these rivers, mussels occur at local (stream reach) scales as distinct beds in depositional areas where shear stresses are low and sediments stable during high flows (Strayer 1999, Strayer et al. 2004). We selected a priori 21 mussel beds from three rivers (Little, Kiamichi, and Ouachita rivers) for which we had existing information on mussel bed size,

species composition and density, and habitat parameters (Vaughn and Spooner 2006). Most mussel species are found throughout the region, thus mussel beds have similar regional species pools. Therefore, we defined local patches or sites as individual mussel beds, and the regional species pool as the set of all sites combined.

At each site we hand excavated 15 randomly placed 0.25-m² quadrats to a depth of ~20 cm to estimate population densities and performed one person-hour snorkel searches to estimate species richness (S) (Strayer and Smith 2003). Mussels were identified, measured (length), and returned to the bed alive. We used species-specific shell length-wet weight regressions to estimate mussel biomass for all sampled individuals; regression equations were derived from previous measurements taken over multiple sampling sites and dates (Spooner 2007).

Mussel species were lognormally distributed at all sites, with the four most abundant species often accounting for over 70% of biomass. At each site, the four most abundant species were subsampled ($n = 5$) for wet weight, body-condition index (Fulton's K), and mass-specific respiration rates. These measures allowed nonlethal examination of species performance at two scales of inference: Fulton's K characterizes energy integration throughout a mussel's life span, while mass-specific respiration is a more proximate measure of energy assimilation and a rough estimate of secondary production. Previous work found a negative relationship between body condition index and mass-specific respiration rates in mussels in good physiological condition (Paterson 1983, Spooner 2007). Therefore, we consider mussels that have low mass-specific respiration rates and high condition indices as having strong individual performance.

In the field, we recorded wet mass and gently scrubbed mussels to remove biofilm. Mussels were individually placed in containers with 500 mL of GF/F filtered river water, oxygen was measured with a Thermo Orion 835A meter (Thermo Scientific, Waltham, Massachusetts, USA), containers were sealed and placed in the river, left for an hour, and final oxygen concentrations measured. In addition, we had five non-mussel controls. Mass-specific respiration rates (MSR) for each individual were calculated as the oxygen consumed per hour corrected for water volume, mussel biomass (wet mass including shell), and change in oxygen in control treatments. Body condition index (Fulton's K), hereafter BCI, was calculated as the entire wet mass of a mussel divided by (shell length)³ × 10⁶ (Mgaya and Mercer 1995). Mussels were returned alive to the mussel bed after measurements were completed.

Thermal niches

We used measures of spatial and temporal thermal variation as an index of the number of available thermal niches per site. We quantified temperature at the sediment–water interface of each quadrat (digital thermometer [±0.01°C]) and calculated spatial thermal

variation as the variance in temperature among quadrats ($n = 15$) for each site. We also recorded water temperature (±0.01°C) every 4 hours at each site for one month (August 2005) with Hobo data-loggers (Onset Corporation, Bourne, Massachusetts, USA). Temporal thermal variation was calculated as the variance of all observations ($n = 180$) for each site. Sites that experienced higher thermal variation (temporal and spatial) were assumed to have a greater number of thermal niches available to mussels.

Quantification of biodiversity effect

In a departure from typical plot-style diversity experiments, Cardinale et al. (2005) used additive, species-specific regional production estimates to predict local diatom community biomass, in essence comparing site-specific production against that expected in a "typical" community. This approach, along with diversity partitioning approaches, works well for fast-growing, short-lived organisms where primary and secondary productivity are easily measured (Long et al. 2007); however, estimating productivity of long-lived organisms within relevant time frames is difficult. We modified Fox's (2005) technique to partition biodiversity effects on mussel bed standing crop biomass; however, instead of building additive models based on monoculture, we estimated expected yields using pooled regional data for each species similar to Cardinale et al. (2005). Thus, our null hypothesis was that regional factors influencing the colonization and growth of mussels are identical to local factors and therefore the local proportion of mussel species biomass should track the regional proportion of species biomass. If the null hypothesis is falsified, then we can infer that either local processes, including species trait expression, and/or species interactions are important to the differential growth of mussels within an assemblage, or that the distribution of propagules to local patches (mussel beds) is asymmetrical from the regional species pool.

We defined the following for each site (modified from Fox [2005]):

$$\Delta Y = Y_O - Y_E$$

$$\text{NBE} = \underbrace{N(\overline{\Delta \text{RY}})(\overline{M})}_{\substack{\text{Trait-independent} \\ \text{complementarity}}} + \underbrace{N\text{cov}\left(M, \text{RY}_O - \frac{\text{RY}_O}{\text{RYT}_O}\right)}_{\substack{\text{Trait-dependent} \\ \text{complementarity}}}$$

$$+ \underbrace{N\text{cov}\left(M, \frac{\text{RY}_O}{\text{RYT}_O} - \text{RY}_E\right)}_{\text{Dominance effect}}$$

where Y_O is the observed total yield (total community biomass), and Y_E is the expected total yield (total expected community biomass) of all mussel species at a given site. The expected total yield Y_E was calculated as

the sum of the regional average biomass across all sites for each species. The net biodiversity effect (NBE) was calculated as the sum of trait-independent complementarity, trait-dependent complementarity, and dominance effects. The deviation in relative yield (ΔRY) was calculated as the difference in relative observed (RY_O) and relative expected yield (RY_E). RY_O for a given species was quantified as the observed biomass of that species at a given site divided by its predicted mean regional biomass (M). Predicted mean regional biomass (M) was calculated as the average biomass for a particular species across all sites. RY_E was calculated for each species as M divided by the sum of M for all other species occurring at a site. Previous estimates of RY_E in terrestrial systems have been quantified as the initial planted abundance divided by the total planted abundance of the mixture (Loreau 1998). Our RY_E relationship is based on the null hypothesis that the relative expected biomass of a species at a given site is a function of its regional abundance.

Data analyses

For each site, the four sampled species were subdivided into two groups. The two most numerically abundant species at a given site were considered "major" species and their biomass was averaged, while the other two species were considered "minor" species and their biomass averaged. We recognize that our use of "minor" species does not necessarily characterize the rarest possible species at a particular site. However, given the lognormal distribution of species abundance within sites, it was not possible to consistently find five replicate individuals of the rarest species. Thus, we used the third and fourth most abundant species to ensure adequate replication and consistent sampling across sites.

We used linear correlation to evaluate the influence of site species richness (S), spatial thermal variation, and temporal thermal variation on ΔY, net biodiversity effect, TI complementarity, TD complementarity, and dominance effect. Estimates of S combined both quadrat and timed search results. We also examined the influence of diversity effects (richness, TI complementarity, TD complementarity, and dominance) and niche variability (spatial and temporal variation) on body condition index (BCI) and mass-specific respiration rates (MSR). Values of TI complementarity, TD complementarity, and dominance effect were square-root transformed (with signs preserved) to meet parametric assumptions of homogeneity. For each linear correlation, randomization techniques were used to test the null hypothesis that the slope, intercept, and correlation coefficient were not different from zero. Statistical analyses were performed with EcoSim software (version 7; Gotelli and Entsminger 2007).

RESULTS

Mussel species were lognormally distributed both regionally and locally. Three species, *Actinonaias liga-*

mentina (Lamarck 1819), *Amblema plicata* (Say 1817), and *Quadrula pustulosa* (Lea 1831) contributed the largest proportions of biomass to the mussel assemblages, respectively. As expected, the net biodiversity effect and ΔY were highly correlated ($r = 0.892$, $P < 0.001$), so graphical results are only presented for ΔY (Fig. 1A). Overall, both ΔY ($r = 0.467$, $P = 0.004$) and the net biodiversity effect ($r = 0.469$, $P = 0.009$) increased with species richness but appeared to be influenced by one site with a disproportionate amount of biomass. These correlations remained significant after performing the analysis with the biomass-rich site removed (ΔY, $r = 0.362$, $P = 0.042$; NBE, $r = 0.219$, $P = 0.021$).

Partitioning

Across all sites, TI complementarity contributed the greatest fraction of the net biodiversity effect (38.2–73.5%), followed by TD complementarity (11.3–44.1%) and dominance effect (6.8–42.3%). TI complementarity ($r = 0.775$, $P < 0.001$) increased positively with species richness (Fig. 1B), suggesting that mussel species in species-rich beds have greater biomass than regionally expected. There was no relationship between TD complementarity and species richness ($r = -0.551$, $P = 0.650$; Fig. 1B). The dominance effect was negative and decreased with increasing species richness ($r = -0.705$, $P = 0.002$; Fig. 1B, Table 1).

TI complementarity was highest at sites with high spatial ($r = 0.542$ $P = 0.011$; Fig. 1C) and temporal ($r = 0.311$, $P = 0.053$; Fig. 1D) thermal variation, while TD complementarity was related to spatial ($r = 0.428$, $P = 0.040$; Fig. 1C) but not temporal thermal variation ($r = -0.045$, $P = 0.602$; Fig. 1D). The dominance effect became increasingly negative as a function of spatial ($r = -0.366$, $P = 0.045$; Fig. 1C) and temporal thermal variation ($r = -0.377$, $P = 0.039$; Fig. 1D, Table 1).

Condition

TI complementarity was not related to body condition (BCI; $r = -0.224$, $P = 0.150$; Fig. 2A) or mass-specific respiration ($r = 0.207$, $P = 0.181$; Fig. 2D) of major species; however, minor species body condition correlated positively ($r = 0.382$, $P = 0.039$; Fig. 2A) and mass-specific respiration correlated negatively ($r = -0.337$, $P = 0.048$; Fig. 2D) with TI complementarity (Table 1).

TD complementarity correlated positively with major species body condition index ($r = 0.356$, $P = 0.052$; Fig. 2B) and negatively with mass-specific respiration ($r = -0.487$, $P = 0.009$; Fig. 2E), supporting the prediction that major species should have higher condition at sites with a higher TD complementarity. In addition, there was no significant relationship between minor species body condition index ($r = 0.182$, $P = 0.253$; Fig. 2B) or mass-specific respiration ($r = 0.052$, $P = 0.399$; Fig. 2E) and TD complementarity, indicating that this added benefit to major species did not negatively influence the condition of minor species (Table 1).

There was not a significant relationship between the dominance effect and major species body condition ($r =$
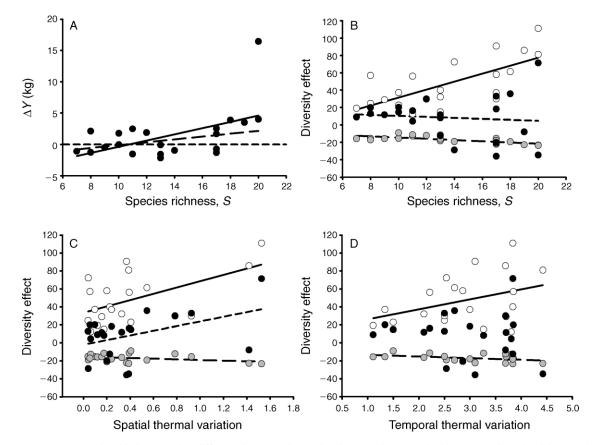
Fig. 1. (A) Relationship between ΔY (difference between observed and expected community biomass) and species richness. The solid line represents the relationship including the extreme data point ($r = 0.467$, $P = 0.004$), and the dashed line represents the significant relationship without the extreme data point ($r = 0.362$, $P = 0.042$). The dotted line indicates zero diversity effect. (B–D) Relationship between diversity effect and (B) species richness (trait-independent complementarity [TIC], $r = 0.775$, $P < 0.001$; trait-dependent complementarity [TDC], $r = -0.551$, $P = 0.650$; dominance effect [Dom], $r = -0.705$, $P < 0.001$); (C) spatial thermal variation (TIC, $r = 0.542$, $P = 0.011$; TDC, $r = 0.428$, $P = 0.040$; Dom, $r = -0.366$, $P = 0.045$); and (D) temporal thermal variation (TIC, $r = 0.311$, $P = 0.053$; TDC, $r = -0.045$, $P = 0.60$; Dom, $r = -0.377$, $P = 0.039$). Open circles with solid lines are trait-independent complementarity, black circles with short-dashed lines are trait-dependent complementarity, and gray circles with long-dashed lines are dominance species effects. All values were square-root transformed and signs preserved.

TABLE 1. Predicted and observed relationships between diversity effects (trait-independent complementarity, trait-dependent complementarity, dominance), species richness, thermal variation (spatial and temporal), and condition measures (Fulton's K and mass-specific respiration [mg $O_2 \cdot$g wet mass$^{-1} \cdot L^{-1} \cdot h^{-1}$]) for abundant (major) and rare (minor) species.

Independent variable	Major			Minor		
	Dependent variable	Predicted	Observed	Dependent variable	Predicted	Observed
Trait-independent complementarity (TIC)	Fulton's K (BCI)	+	0	Fulton's K (BCI)	+ *	+ *
	Respiration (MSR)	−	−	Respiration (MSR)	− *	− *
Trait-dependent complementarity (TDC)	Fulton's K (BCI)	+ *	+ *	Fulton's K (BCI)	0	0
	Respiration (MSR)	− *	− *	Respiration (MSR)	0	0
Dominance effect (Dom)	Fulton's K (BCI)	0	0	Fulton's K (BCI)	− *	0 *
	Respiration (MSR)	−	0	Respiration (MSR)	+	+
Species richness	Fulton's K (BCI)	+	0	Fulton's K (BCI)	+ *	+ *
	Respiration (MSR)	−	0	Respiration (MSR)	− *	− *
Spatial thermal variation	Fulton's K (BCI)	0	0	Fulton's K (BCI)	+ *	+ *
	Respiration (MSR)	0	0	Respiration (MSR)	− *	− *
Temporal thermal variation	Fulton's K (BCI)	0	0	Fulton's K (BCI)	+ *	+ *
	Respiration (MSR)	0	0	Respiration (MSR)	− *	− *

Note: Symbols represent the direction of the relationship (+, positive relationship; −, negative relationship; 0, no relationship).
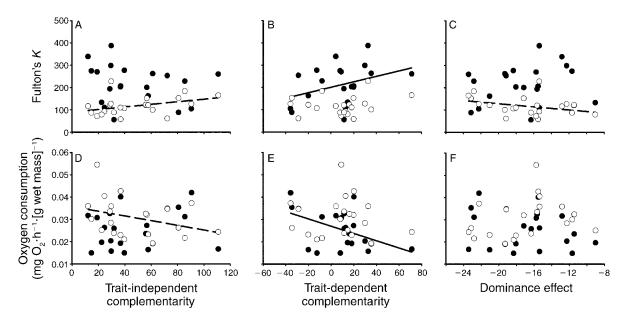* $P < 0.05$.

FIG. 2. The top row of panels depicts the relationship between body condition index (Fulton's K) and (A) trait-independent complementarity (numerically dominant [major] species, $r = -0.224$, $P = 0.150$; numerically subordinate [minor] species, $r = 0.382$, $P = 0.039$), (B) trait-dependent complementarity (major, $r = 0.356$, $P = 0.052$; minor, $r = 0.182$, $P = 0.253$), and (C) dominance species effect (major, $r = 0.141$, $P = 0.268$; minor, $r = -0.352$, $P = 0.056$). The bottom row of panels shows the relationship between mass-specific respiration and (D) trait-independent complementarity (major, $r = 0.207$, $P = 0.181$; minor, $r = -0.337$, $P = 0.048$); (E) trait-dependent complementarity (major, $r = -0.487$, $P = 0.009$; minor, $r = 0.052$, $P = 0.399$); and (F) dominance species effect (major, $r = -0.288$, $P = 0.146$; minor, $r = 0.279$, $P = 0.115$). Solid circles with solid lines represent major species, and open circles with dashed lines represent minor species.

0.141, $P = 0.268$; Fig. 2C) or mass-specific respiration ($r = -0.228$, $P = 0.146$; Fig. 2F), indicating that there is no quantifiable physiological benefit to major species as the dominance effect increases. Although they were not statistically significant, mass-specific respiration increased ($r = 0.279$, $P = 0.115$; Fig. 2F) and minor species body condition (BCI) marginally decreased ($r = -0.352$, $P = 0.056$; Fig. 2C) with greater dominance effects (Table 1).

Thermal niches

There were no significant relationships between condition (BCI, MSR) of major species and species richness (BCI, $r = 0.042$, $P = 0.413$, Fig. 3A; MSR, $r = -0.169$, $P = 0.242$, Fig. 3D), spatial thermal variation (BCI, $r = 0.247$, $P = 0.149$, Fig. 3B; MSR, $r = -0.274$, $P = 0.110$, Fig. 3E), or temporal thermal variation (BCI, $r = 0.307$, $P = 0.093$, Fig. 3C; MSR, $r = 0.053$, $P = 0.588$, Fig. 3F) indicating that there is little energetic benefit for major species living in speciose, thermally variable sites (Table 1). Minor species did benefit from living within species-rich communities (BCI, $r = 0.514$, $P = 0.006$, Fig. 3A; MSR, $r = -0.608$, $P < 0.001$, Fig. 3D). Furthermore, minor species' condition was significantly associated with spatially (BCI, $r = 0.672$, $P = 0.004$, Fig. 3B; MSR, $r = -0.402$, $P = 0.026$, Fig. 3E) and temporally (BCI, $r = 0.729$, $P < 0.001$, Fig. 3C; MSR, $r = -0.419$, $P = 0.034$, Fig. 3F) variable environments (Table 1).

DISCUSSION

Freshwater mussel communities dominate large fractions of benthic biomass in some rivers, linking pelagic and benthic compartments and serving as effective nutrient and energy pumps. Thus, the nature of interactions between community assembly, environmental context, and mussel biomass accrual within these communities should have important consequences to stream ecosystem function. Our results demonstrate that mussel biomass in species-rich communities is substantially higher than that predicted by the average biomass of species across the region. In addition, TI complementarity accounted for the highest fraction of the net biodiversity effect, suggesting that this increased biomass is associated with the performance of the entire mussel community rather than the supremacy of a few dominant species.

TI complementarity effects were positive and increased with species richness, suggesting that mussels perform better in a species-rich arena. That TI complementarity accounted for the highest fraction of the net biodiversity effect also indicates that niche differences between species may be an important factor governing the growth and potential fitness of mussels. Strong, positive associations between richness, abundance, and habitat quality are well demonstrated in a variety of systems (MacArthur et al. 1966), and are usually related to the degree of habitat heterogeneity (Tews et al. 2004). Consequently, it's generally assumed
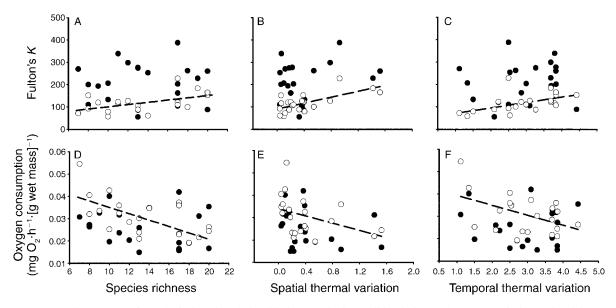
FIG. 3. The top row of panels depicts the relationship between body condition index (Fulton's K) and (A) species richness (numerically dominant [major] species, $r = 0.042$, $P = 0.413$; numerically subordinate [minor] species, $r = 0.514$, $P = 0.006$), (B) spatial thermal variation (major, $r = 0.247$, $P = 0.149$; minor, $r = 0.672$, $P = 0.004$), and (C) temporal thermal variation (major, $r = 0.307$, $P = 0.093$; minor, $r = 0.729$, $P < 0.001$). The bottom row of panels shows the relationship between oxygen consumption and (D) species richness (major, $r = -0.169$, $P = 0.242$; minor, $r = -0.608$, $P < 0.001$), (E) spatial thermal variation (major, $r = -0.274$, $P = 0.110$; minor, $r = -0.402$, $P = 0.026$), and (F) temporal thermal variation (major, $r = 0.053$, $P = 0.588$; minor, $r = -0.419$, $P = 0.034$). Solid circles are major species, and open circles with dashed lines are minor species.

that species sharing high degrees of overlap somehow partition resources along one or more niche axes, limiting competition for resources and maximizing growth and fitness. However, despite occurring as speciose, spatially clumped aggregations, freshwater mussels share surprisingly broad, overlapping resource requirements and there is little evidence that species partition the traditional niches of habitat structure, space, or diet (Vaughn and Hakenkamp 2001, Strayer et al. 2004, Vaughn et al. 2008). Studies that have demonstrated differences in habitat use have either done so at coarse habitat scales (lentic vs. lotic systems [Silverman et al. 1997]) or by correlating measures of habitat stability (shear stress and slope) with species richness; these measures however, often relate to the presence or absence of mussel communities, and poorly predict mussel richness. On the other hand, most mussel larvae (glochidia) are obligate ectoparasites on fish and vary in host specificity and attraction strategies (Haag and Warren 1998). Watters (1993) hypothesized that host-fish partitioning resulting from elaborate host attraction strategies and reproductive timing could explain species coexistence. This hypothesis is supported by strong mussel-fish richness relationships at the watershed scale, but fails to explain direct physiological benefits within communities (Watters 1993).

Spooner (2007) found that co-occurring mussel species differentially acquire and assimilate resources under varying temperatures. We found that TI complementarity was highest at sites with the greatest spatial and temporal thermal variation, supporting our hypoth-

esis that mussels may occupy different "thermal niches" and partition resources along thermal gradients. The concept of temperature as a mediator of resource use has a long history (Magnuson et al. 1979), and is gaining considerable attention in light of predicted effects of climate change on ecosystems (McMahon and Hays 2006). While partitioning of thermal habitat primarily has been shown to be important in xeric plant (Martin 2001) and marine (Attrill and Power 2004, Krassoi et al. 2008) communities, the temperature gradient in mid-western/southern streams can be just as steep, and less predictable (daily and seasonally) (Matthews et al. 2005).

If niche differences were the only mechanisms by which different species acquired and assimilated energy, we would expect an additive relationship between ΔY (observed minus expected biomass) and species richness (Cardinale et al. 2005). For example, if different mussel species occupied diverse substrate types or used different food resources, the added presence of those species in a community should be a function of locally added habitat heterogeneity (Loreau 2000). Our results demonstrate that the deviation in observed biomass to predicted biomass (ΔY) increases as a function of species richness, which suggests that in addition to niche complementarity, facilitative interactions also may be important (Cardinale et al. 2002). The importance of environmental context on the nature of facilitation is well-documented in marine and plant communities (Bertness and Hacker 1994). For example, Callaway and King (1996) experimentally manipulated soil temperature in

plant communities and found that at 11–12°C, *Typha latifolia* benefited neighboring plants by increasing soil oxygen, yet exerted strong competitive interactions inhibiting plant growth at 20°C (Callaway and King 1996). Mussel assemblages, through suspension feeding, excretion and biodepositon, transfer energy from the water column to the sediment which in turn influences the abundance and diversity of non-bivalve invertebrates in the benthos (Spooner and Vaughn 2006, Vaughn et al. 2008), although more research is needed on how these processes influence co-occurring mussels. For example, mussel burrowing activities and shell architecture may increase flow heterogeneity and resource transfer to other mussels in a manner similar to other assemblages of filter feeders, such as caddisfly communities (Cardinale et al. 2002, Vaughn et al. 2008). Thus, thermal variation in mussel beds may differentially influence mussel activity and lead to increased facilitative interactions (e.g., resuspension and/or co-prophagy of food, decreased metabolic costs associated with resource capture and respiration).

If the dominance effect and TD complementarity were truly analogous to natural selection, we would expect selection to favor major species' traits at sites where major species grow optimally. Therefore, we would expect the magnitude of dominance and TD complementarity effects to increase at sites that match the optimal temperature of major species, not the variation around the mean. Our results loosely support this prediction as the dominance effect was unrelated to spatial and temporal thermal variation. TD complementarity, however, was unrelated to temporal thermal variation, and became more negative at sites with increased spatial thermal variation. Negative TD complementarity effects occur when regionally rarer species perform better without influencing dominant species, which we would expect to be related to thermal variation.

We recognize that our results demonstrate a lack of a relationship between dominant species effects and temperature, and thus only weakly support our predictions. Longer-term average temperature data or species-specific degree-day estimates are required to rigorously evaluate whether major species arise at sites that match their optimal growth. However, we have laboratory data that indirectly support our hypothesis. Spooner (2007) manipulated the relative abundance of mussel species under different thermal regimes and found that species at their physiological thermal optima had the greatest impacts on ecosystem services and the largest influence on the performance of other species. Further, the two species in the experiment that had the most divergent physiological response to temperature and greatest ecosystem effects (*Actinonaias ligamentina* and *Amblema plicata*), were also the two most dominant species found across sites in our study.

Freshwater mussels are long lived (25–100 yr), thus it is difficult to directly quantify changes in growth rates and fitness under experimental time frames to potentially detect species interactions. This study partitioned the influence of diversity on standing crop biomass (used as a surrogate for secondary production) of mussel assemblages. This pattern represents a "snapshot in time" and could reflect current or historical species interactions. Since mussels are iteroparous and reproduce when an energy threshold is met (Bauer 1998), we used body condition (BCI) as an indirect indicator of fitness and quantified mass-specific respiration to estimate relative rates of energy uptake as a proximate measure of secondary production. We predicted that major and minor species at sites exhibiting higher TI complementarity should have higher body condition and lower mass-specific respiration. We found a strong positive relationship between minor species body condition and TD complementarity, implying that minor species living in a speciose assemblage are in better condition and potentially have higher fitness. Additionally, there was a strong negative relationship between mass-specific respiration of minor species and TI complementarity, indicating that there is some energetic benefit to living in a speciose assemblage. Despite these strong findings, there was no relationship between TI complementarity and major species condition, indicating that other factors may influence major species growth and fitness.

We predicted that the condition of major species should increase at sites with high TD complementarity effects, without influencing minor species. Our results support this prediction as major species had increased body condition and reduced respiration rates without influencing minor species condition. This suggests that one-way complementarity related to other potential niche axes or thermal modes may be important to community dominance. We found no relationship between body condition or mass-specific respiration of major species and dominance effects; however, the magnitude of both dominance and trait-dependent complementarity were negligible compared to TI complementarity; thus, we would expect this relationship to be weak. Bruno et al. (2006), using Fox's partitioning technique, found strong species identity effects in marine algae communities suggesting that competitive interactions with dominant species suppressed the effects of species richness. While our study indicated a different mechanism explaining community biomass (TI complementarity opposed to dominance effect), both studies found that negative dominance and distinctive species effects (TD complementarity) increased in magnitude with species richness. This can be interpreted as the most productive species in monoculture (or regionally abundant in our case) performing progressively worse with increased species richness. Indeed, if species-rich communities are associated with higher niche variability, then we would expect the monopoly that major species hold over others to decrease as other niches become available and their competitive advantage decreases.

Our results support this hypothesis as the condition of minor species (lower BCI) declined at sites with increased dominance effects.

Recent studies have demonstrated that recruitment limitation and propagule pools operate at a variety of spatial scales, differentially influencing the nature of biodiversity–ecosystem function relationships (Bond and Chase 2002, Foster and Dickson 2004). We assumed that local propagule settlement was a lottery function, and that species colonization occurs as a direct proportion of the regional species pool. This assumption implies that upon settlement, trait expression and species interactions between propagules interactively dictate the acquisition, assimilation, and thus relative growth between individuals. These interactions, coupled with the synchrony of propagule traits and the surrounding environment, alter the relative distribution of species biomass compared to the regional model. Alternatively, a similar pattern may arise if mussel beds themselves altered the nature of settlement, allowing a higher proportion of propagules to settle within species-rich mussel beds. Several studies have documented a strong, positive correlation between mussel and fish species richness but stop short of determining any direct mechanism for this relationship (Watters 1993, Vaughn and Taylor 2000). One hypothesis is that mussel communities are self-organizing, i.e., mussels alter habitat (substrate stability, food availability) in a manner that favors fish recruitment and succession over time, which in turn, facilitates recruitment of new mussel species via their fish hosts (Strayer et al. 2004). Species-rich mussel beds may increase the encounter rate of propagules by attracting novel fish, favoring colonization and growth of more juveniles. Although this mechanism could explain the increased abundance of mussels in species-rich beds, it does not explain their increased body condition or reduced respiration rates; thus other mechanisms, including species interactions should still play a prominent role.

All approaches to addressing ecological questions come with specific benefits and caveats. Manipulative experiments can be robust in establishing causal relationships and are integral for identifying mechanisms, but are typically limited in their applicability to natural systems. This study complements current experimentally derived biodiversity–ecosystem function research by applying recent theoretical approaches to natural communities, but should be tempered with the understanding that the results of this approach are correlative. Nonetheless, this research emphasizes the importance of species interactions and environmental context in understanding the structure and functioning of ecosystems.

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